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Relationship Between Food Supply and Condition of Wild Brown Trout, *Salmo trutta* Linnaeus, in a Michigan Stream

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ABSTRACT

Field study revealed great differences in the biological productivity of two adjacent areas of a Michigan trout stream resulting from the entrance of domestic sewage into the stream between the two areas. Monthly samples were collected from the two areas to determine the seasonal cycles in abundance of bottom fauna, feeding habits of the trout, and coefficient of condition of the brown trout. In the less productive area upstream, a paucity of food of aquatic origin caused a sharp decline in condition of the fish, a reduction in the quantity of food per stomach, and a shift to a diet containing a considerable portion of terrestrial organisms. In the more productive area downstream (which, throughout the year, had a greater volume of bottom fauna than the unproductive area) trout maintained a significantly higher and much less variable coefficient of condition, their stomachs contained more food in midsummer and did not show the increase in terrestrial foods.

INTRODUCTION

The length-weight ratio or coefficient of condition of stream trout varies during the year (Went and Frost 1942, Cooper and Benson 1951, Cooper 1953), and moreover this ratio is related to growth in that fish which are relatively heavy are growing faster than fish which are relatively light (Went and Frost 1942, Allen 1940, and Brown 1946a). Thus, coefficient of condition is a useful measurement in studies of trout populations; because it marks the season when growth is most rapid, and is a means for comparing the relative well-being of the fish.

Brown (1946a) reported that brown trout reared in the laboratory under constant conditions of food, light, and temperature exhibited an annual growth-rate cycle and that the rate of growth in length was directly proportional to the condition of the fish. Benson (1954), Allen (1940), and Neill (1938) demonstrated a direct correlation between volume of stomach contents and seasonal changes in condition for brook

trout, young salmon, and brown trout in a natural stream environment. Allen (1940) found no correlation between growth of stream fish and seasonal abundance (but not volume) of food.

Although the seasonal change in condition in the salmonids has been established repeatedly, its cause has remained uncertain. Field study during 1950 and 1951 revealed great differences in the standing crop of bottom organisms of two adjacent portions of Houghton Creek, a trout stream in Michigan. This situation offered an opportunity to investigate the correlation between differing food supplies and the condition factor and growth of native brown trout in the two stream sections.

Appreciation is extended to Dr. David C. Chandler, Department of Zoology, University of Michigan, and to Dr. Frank F. Hooper, Institute for Fisheries Research, who read the paper critically. Mr. Walter R. Crowe gave freely of his time in editing the paper. Other members of the staff of the Institute for Fisheries Research aided in sampling the trout populations.

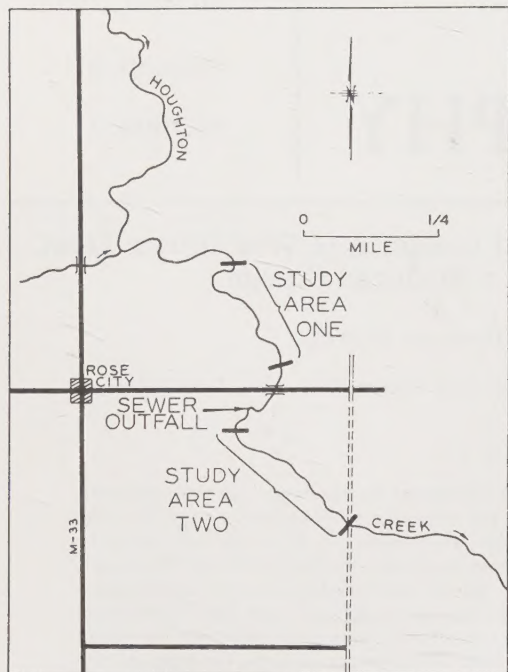


FIG. 1. Map of Houghton Creek, Ogemaw County, Michigan, showing relationships between study areas and sewer outfall.

STUDY AREA

Houghton Creek, Ogemaw County, Michigan, is approximately 9.7 miles long and is a tributary of the Rifle River (Fig. 1). The village of Rose City (population 500), located about midway between source and mouth of the stream, discharges untreated sewage into Houghton Creek. A survey conducted by the Michigan Water Resources Commission in August and October, 1950, to determine the degree of pollution of the stream by sewage from Rose City revealed a maximum biochemical oxygen demand of 3.6 ppm coincident with a supply of dissolved oxygen of 9.8 ppm at a temperature of 56°F. The Commission concluded that the sewage did not decrease the oxygen sufficiently to harm fish. The same conclusion was reached in a re-survey in October of 1956.

The study was conducted in two areas. Area One began 1,300 feet above the sewer outfall and extended upstream 1,734 feet; Area Two started 300 feet below the out-

fall and extended downstream 1,900 feet (Fig. 1).

Physically, the two sections of stream were similar. Area One had an average width of 24 feet and an average depth of 1.1 feet; Area Two averaged 24.4 feet in width and 1.6 feet in depth. The proportion of each type of bottom soil and amount of cover suitable for trout appeared to be the same at both sites. Water temperatures were in close agreement in the two sections, and these temperatures were nearly identical with those recorded on a thermograph housed in a gaging station on Houghton Creek 5.5 miles downstream from the sewer outfall. Mean maximum and minimum water temperatures recorded at this gaging station during the period of this study are shown in Figure 2.

The few chemical analyses made revealed little difference between the two sections, except for additional nitrogen and phosphorus in Area Two resulting from the sewage (Table 1). Two water samples collected during preliminary investigations were found to have chloride concentrations which averaged 1.5 ppm for Area One and 3.0 ppm for Area Two. These concentrations of chloride indicated a limited amount of pollution from the sewage.

BOTTOM FAUNA

A modified Surber sample was used to collect samples of bottom fauna for quantitative and qualitative analysis. For practical reasons all samples were collected from riffle areas. Four 1/2-square-foot samples were collected at each of two sites in each study area at monthly intervals from August through December 1953 and April through May 1954. In June 1954 only one site was sampled in each area because of flood waters. Organisms were sorted out of the bottom samples, and the total volume of all organisms in each sample was determined by displacement of fluid in a 15-ml centrifuge tube.

The results of the sampling are summarized in Table 2 and Figure 2. The three categories presented in the table were used for convenience of presentation and

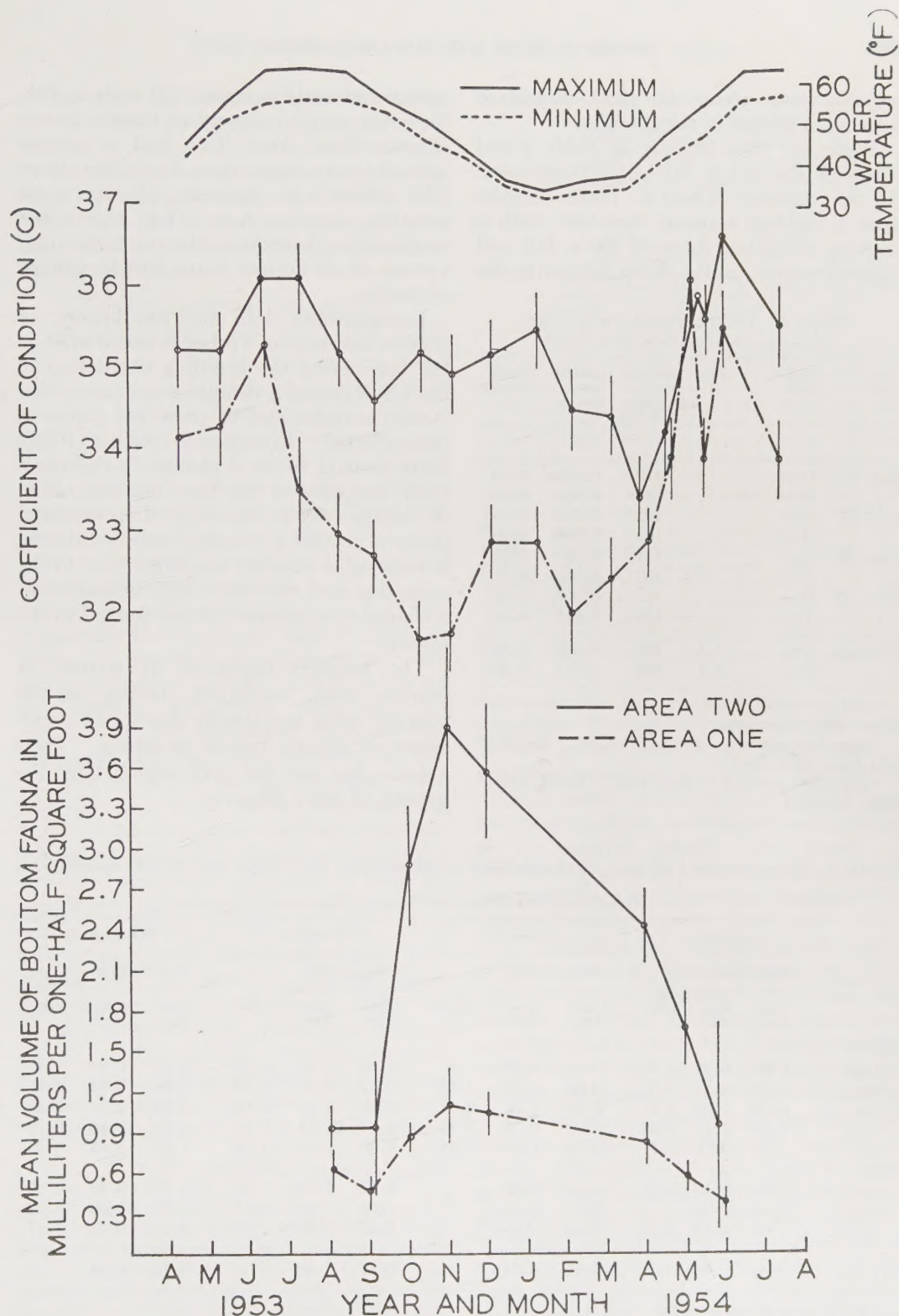


FIG. 2. Seasonal variation of water temperature (monthly averages), of condition (C) of wild brown trout, and of bottom fauna abundance in Houghton Creek, Ogemaw County. Vertical line represents two standard errors above and below the mean for coefficient of condition, and one standard error for abundance of bottom fauna.

because these were the most important taxonomic groups in the samples.

There are three aspects of Table 2 and Figure 2 that are of particular importance: (1) the volumes of bottom fauna samples show a marked seasonal variation, with a summer minimum followed by a fall and winter increase, and a sharp decline in the

spring and early summer; (2) each month, for every major category of bottom fauna, samples from Area Two had a greater volume than samples from Area One (except "All others" in August); (3) for most monthly samples Area Two was richer statistically than Area One in both total volume of all bottom fauna and in volume of *Asellus*.

Investigations into the life history of *Asellus intermedius* Forbes revealed that in the late spring the breeding population of the riffles makes a definite migration to the stream margins and to protected places in deeper water. As suggested by Allee (1912), there seemed to be a change in the rheotactic response of the breeding population of *Asellus*. Thus the sharp drop in abundance of *Asellus* in samples collected during late spring or summer was largely due to the migration and was not a true indication of a change in abundance of this animal in the stream.

The summer minimum in volume of bottom fauna, excluding *Asellus*, in the gravelly riffles was largely due to the emergence of aquatic insects as adults. Their volume had not yet been replaced by the growth of their offspring.

TABLE 1. Chemical analysis of water from two areas of Houghton Creek

Date 1953	Study area	pH ¹	Methyl orange alkalinity as CaCO ₃	Soluble ² phosphorus	Total ³ nitrogen
ppm					
July 2	One	...	172	0.008	0.60
	Two	...	164	0.004	0.68
July 31	One	...	161	0.005	0.08
	Two	...	164	0.049	0.20
Aug. 25	One	...	171	0.005	0.45
	Two	...	169	0.009	0.57
Nov. 27	One	...	172	0.002	0.57
	Two	...	176	0.012	0.80
Average	One	8.4	169	0.005	0.425
	Two	8.3	168	0.018	0.562

¹ pH determinations were not coincident with other determinations.

² Ceruleomolybdic method (Ellis, Westfall, and Ellis 1948: 79-81).

³ Kjeldahl method (Amer. Publ. Health Assoc. 1955: 155-157).

TABLE 2. Mean volumes (ml per $\frac{ft^2}{2}$) of eight $\frac{ft^2}{2}$ bottom samples collected in each of eight months from Houghton Creek, Ogemaw County, Michigan

Date	<i>Asellus</i> ²			<i>Gammarus</i> ²			All others ²			Entire sample		
	Mean volume			Mean volume			Mean volume			Mean volume		
	Area One	Area Two	<i>t</i> value	Area One	Area Two	<i>t</i> value	Area One	Area Two	<i>t</i> value	Area One	Area Two	<i>t</i> value
1953												
Aug.	0.04	0.29	3.45	trace	0.08	...	0.58	0.56	0.04	0.62	0.93	1.47
Sept.	0.04	0.34	2.58	0.01	0.08	2.26	0.42	0.52	2.20	0.48	0.93	2.23
Oct.	0.08	1.02	3.77	0.03	0.33	2.58	0.76	1.57	3.02	0.86	2.88	8.23
Nov.	0.09	1.47	3.39	0.01	0.28	2.49	1.01	2.14	2.46	1.11	3.89	3.79
Dec.	0.11	0.96	3.77	0.03	0.08	1.41	0.89	2.49	4.15	1.03	3.53	4.35
1954												
Apr.	0.01	0.49	3.12	trace	0.02	...	0.77	1.89	3.85	0.78	2.40	4.67
May	trace	0.03	...	0.0	trace	...	0.53	1.60	2.75	0.53	1.63	3.72
June ¹	0.01	0.04	0.85	trace	trace	...	0.37	0.89	1.36	0.38	0.93	1.17
Average	0.05	0.58		0.01	0.11		0.67	1.46		0.72	2.14	

¹ N = 4 for June only; all other N = 8.

² *Asellus* = *A. intermedius* Forbes; *Gammarus* = *G. fasciatus* Say; other = over 90 per cent aquatic insects.

t values were calculated according to Dixon and Massey 1951: 104.

The most important difference between the two study areas was the greater supply of aquatic food in the lower section (Area Two) during the summer. In summer, when the supply of other aquatic foods was low, *Asellus* and *Gammarus* were much more numerous in the area below the sewer out-fall than above.

COEFFICIENT OF CONDITION

Samples of 100 brown trout, 5.0 inches (127 mm) or more in total length, were collected in each area at approximately monthly intervals from April 17, 1953 to April 29, 1954, and at approximately semi-monthly intervals from April 15 to July 13, 1954 (Table 3). All samples were collected with electro-fishing gear powered by a 220-volt direct-current generator. The fish were returned to the stream after they had been weighed and measured.

Average coefficients of condition (C)¹ were computed for samples of trout collected in each area during a 16-month period. Results are plotted in Figure 2 and tabulated in Table 3. It will be noted that the seasonal trends in condition improved to a maximum with the advance of spring and declined during the summer months. During fall and early winter the condition factor of the trout again rose before decreasing to a minimum in midwinter or later.²

Earlier studies of salmonids in lotic environments have shown a seasonal trend in condition similar to the one observed in Houghton Creek (Went and Frost 1942, Cooper and Benson 1951, Cooper 1953). In addition Went and Frost (1942) and Cooper (1953) showed a correlation between growth and condition. Periods of rapid growth were associated with high condition, whereas condition was poor during periods of little or no growth. Allen (1940) further

¹ $C = \frac{W \times 10^5}{L^3}$ where W = weight in pounds and L = total length in inches.

² Despite the occurrence of occasional large individuals in some collections, the mean length and length-frequency distribution of fish in the paired samples from the two areas were closely comparable. Variations in coefficient of condition related to length, age, and sex were unimportant as compared to the consistent and much greater areal and seasonal differences observed.

TABLE 3. *Average coefficient of condition (C) of native brown trout in Houghton Creek, Ogemaw County*

Data based on periodic samples of 100 fish 5 inches (127 mm) or more in length

Date	Area One			Area Two			t value
	Size range (inches)	Mean C	Std. error of mean	Size range (inches)	Mean C	Std. error of mean	
4-7-53	5.0-11.7	34.17	0.229	5.0-23.2	35.24	0.249	3.16
5-11-53	5.1-13.8	34.25	0.291	5.0-15.0	35.23	0.224	2.67
6-10-53	5.0-14.0	35.37	0.218	5.0-24.1	36.14	0.273	2.20
7-7-53	5.0-12.3	33.52	0.338	5.0-18.6	36.13	0.264	6.08
8-6-53	5.1-12.1	32.94	0.250	5.0-24.3	35.21	0.243	6.51
9-3-53	5.1-11.5	32.71	0.239	5.5-14.3	34.61	0.202	6.07
10-9-53	5.1-14.5	31.67	0.238	5.0-24.3	35.22	0.258	10.11
11-3-53	5.1-13.1	31.73	0.282	5.0-12.3	34.91	0.251	8.42
12-2-53	5.0-11.6	32.84	0.259	5.0-14.6	35.19	0.246	6.58
1-8-54	5.0-11.6	32.80	0.237	5.0-14.7	35.48	0.260	7.62
2-5-54	5.0-14.5	32.00	0.268	5.0-13.9	34.49	0.279	6.44
3-5-54	5.0-12.3	32.42	0.276	5.0-12.3	34.42	0.252	5.35
3-29-54	5.0-12.1	32.79	0.236	5.0-15.7	33.41	0.281	1.69
4-15-54	5.0-13.0	33.79	0.278	5.0-15.9	34.22	0.320	1.01
5-4-54	5.0-11.9	36.11	0.254	5.0-13.2	35.88	0.297	0.59
5-17-54	5.0-12.0	33.83	0.254	5.1-13.1	35.59	0.228	5.16
6-1-54	5.0-12.1	35.49	0.280	5.0-15.8	36.67	0.332	2.72
7-13-54	5.0-15.0	33.80	0.228	5.0-15.6	35.52	0.282	4.74

found that if condition was low at the onset of the growth period of young salmon, weight increased more rapidly than length, whereas length increased more rapidly than weight if condition was high at the beginning of the growth period. This aspect of growth and condition was corroborated experimentally under laboratory conditions by Brown (1946a).

In comparing the 16-month trend in condition of trout in the two areas, two principal differences are apparent. First, the average condition of trout in Area Two exceeded that in Area One (a single sample excepted). These differences between the average coefficients of condition of trout in the two areas are statistically significant at the 5% level except for the samples of March 29, April 15, and May 4, 1954. Second, the annual range of condition was greater in Area One than in Area Two.

Other features of these seasonal trends in condition are worthy of note. Brown trout in both areas were in poorer condition in early April of 1954 than in April of the preceding year. However, the improvement in condition during April of 1954 was

much more rapid than during April of the previous year. An anomaly occurred between the May and June samples of 1954. The mid-May sample of trout from Area One showed a marked drop in condition over a relatively short period of time while trout from Area Two showed only an insignificant loss of condition.

WATER TEMPERATURE

During the investigation water temperatures in Houghton Creek increased rapidly during April, May, and June, reached a maximum (67°F) in July, and thereafter decreased slowly to a minimum (32°F) in January.

A general upward trend in condition of trout was coincident with an increase in water temperatures during the spring. After attaining the spring maximum in condition, a downward trend in condition preceded a comparable downward trend in water temperature. During a period of slowly falling water temperatures in the fall and early winter, condition of trout tended to recover somewhat. Finally, condition declined to a low during the later half of the winter.

Trout in both areas were subject to similar water temperatures. The influence of water temperature on trout condition was masked somewhat by the effects of other environmental factors. According to Allen (1940) water temperature was the stimulus that initiated activity and growth of salmon smolts in the spring of the year. He cited 7°C (45°F) as the critical water temperature. Brown (1946b) reared two-year-old brown trout at different constant water temperatures and in water of changing temperature and found growth rates to be high between 7° and 9°C (45°–48°F) and between 16° and 19°C (61°–66°F). Above, between, and below these temperatures growth rates were low. In Houghton Creek, the spring rise in the condition factor of brown trout occurred with maximum water temperatures of 41° to 67°F in 1953 and 41° to 61°F in 1954.

Mean minimum and maximum stream temperatures during June (56°–60°F), July (57°–63°F) and August (57°–61°F) were similar. In spite of nearly optimum temperatures for growth during the summer,

the condition of trout in Area One declined after the middle of June, and in Area Two the decline took place during the first week in July. Trout from Area Two maintained better condition than the trout from Area One. Apparently temperature was not the primary cause of the summer decline in the condition factor of these trout.

Sexual maturity appeared to be associated with condition factor values in autumn, particularly during October and November. During this spawning period when water temperatures ranged between 38° and 52°F, mature trout showed a drop in condition, whereas immature trout tended to improve slightly in condition during the late fall months.

During late winter, between the January and late March sampling dates, temperatures ranged between 32° and 42°F. The condition of trout was comparatively poor during this period.

POPULATION DENSITY

To test whether population density might influence the condition factor of trout, estimates of the population of brown trout were made for both stream sections on August 23–24, 1954. A freshwater sculpin (*Cottus* sp.) was the only other species of fish associated with brown trout in these waters. No attempt was made to measure the abundance of freshwater sculpins in the two areas. However, this species was believed to be about equally abundant in both sections of the stream. Area One (1,734 feet in length) was estimated to contain 1,259 brown trout, or about 120 pounds per acre. For Area Two (1,900 feet) the estimate was 1,693 brown trout, or about 127 pounds per acre. Thus the numerical abundance of brown trout was approximately the same in both areas. Size distribution of the trout in the two sections was similar, and all one-inch size groups between 2 and 14 inches were represented in the samples. The effect of population density *per se* on trout condition cannot be discussed here, but evidently population density may be eliminated as a factor accounting for the disparity in condition between trout in the two areas.

FEEDING HABITS, AND UTILIZATION OF
BOTTOM FAUNA

Stomachs from trout in both stream sections were collected to determine if major components of the bottom fauna contributed significantly to the food of trout, and particularly if the abundant *Asellus* was an important item in the diet.

Trout for stomach analyses were collected from each of the two areas with electro-fishing gear. Two stomachs from fish in each one-inch size group (7 through 12 inches) were collected from each area each month from April through August. The stomachs were preserved in 85 per cent alcohol immediately after collection. Only the material in the stomach was examined. Organisms were identified only to the smallest taxonomic group, usually genus, easily recognized by the investigators. Since there is a considerable difference in the rate of digestion of the different kinds of food organisms eaten by trout (Ellis, unpublished), it was felt that a direct volumetric determination of the stomach contents would be invalid, and hence only the number of each kind of organism was recorded.

The results of examination of the stomachs of trout from the two areas is presented graphically in Figure 3. It is readily apparent that the brown trout fed on *Asellus*, and that this animal was possibly a preferred food item. From 33.7 to 87.5 per cent of the organisms contained in the stomachs of trout from Area Two were *Asellus*. For Area One these percentages were 0.8 to 44.7.

The average number of food organisms per stomach (Area One, Fig. 3) shows a marked seasonal decline in July and August, when the fish in this area were directing more effort to surface feeding on terrestrial organisms. This seems to indicate that the supply of food of aquatic origin was low. Parallel collections from Area Two, however, do not show this marked shift to food of terrestrial origin, nor was there a continued reduction in the numbers of food organisms per stomach. This difference in the pattern of feeding seems to indicate that

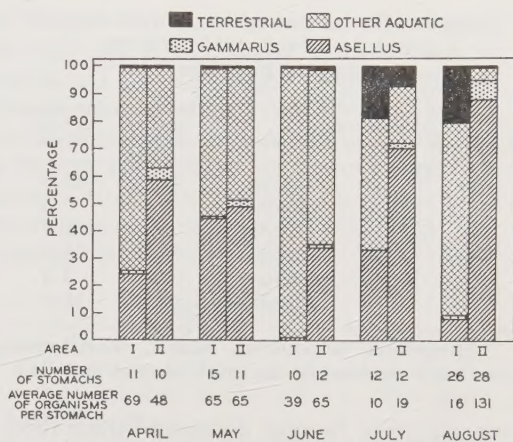


FIG. 3. Numerical abundance (percentage) and number of organisms per stomach for brown trout in Houghton Creek, Ogemaw County.

some difference existed in the food supply of the two areas.

DISCUSSION

Seasonal variation in the volume of bottom fauna has been described frequently. Ball and Hayne (1952) and Eggleton (1931) reported such variations in lakes. Seasonal variation in the volume of stream bottom fauna has also received some attention.

Surber (1937) showed a late spring maximum in volume of bottom fauna in an eastern trout stream, followed by a decline during the summer and a rise during the fall and winter. Needham (1938) reported two maxima in volume of bottom fauna, one in the spring and another in early winter. Allen (1951) described two maxima from the Horokiwi in New Zealand, one in the spring and the other in early winter. In contrast, Pennak and Van Gerpen (1947), found no seasonal periodicity in volume of bottom fauna of a Colorado trout stream. Surber (1951) gave data which indicated no seasonal trend in volume of bottom fauna in a trout stream in Virginia.

In his study of the ecology of streams in Yellowstone National Park, Muttkowski (1925) showed the annual food cycle of mountain trout to be divided into two sharply defined periods. First, the "water food" period of October to July, and second, the "surface food" period of summer. He observed that during the short period of

TABLE 4. *The contents of brown trout stomachs collected in April, 1954, from two study areas in Houghton Creek¹*

Study area	Number of stomachs	Food organisms	Percentage of total numbers	Percentage of total volumes
One	11	<i>Asellus</i>	21.0	48.0
		<i>Gammarus</i>	1.0	0.5
		All others	77.0	51.0
Two	12	<i>Asellus</i>	56.0	78.0
		<i>Gammarus</i>	3.5	3.5
		All others	40.0	18.0

¹ Terrestrial organisms, which contributed less than 1 per cent of the total, are not included.

summer, trout become dependent upon food of terrestrial origin following the depletion of the primary food supply through emergence of insects.

Our data demonstrate a definite seasonal trend in the volume of bottom fauna in gravelly riffles. Bottom fauna was at peak abundance during the winter months and declined gradually until sometime in April. During April and May a sharp reduction in the volume of animals occurred which lasted until early fall when the volume of bottom fauna increased rapidly to a winter high (Fig. 2).

This investigation revealed that the aquatic sowbug, *Asellus intermedius* Forbes, was an important item of difference between the bottom faunas of the two areas. For example, during the August-April period, the volume of *Asellus* in samples from Area Two varied from nearly one-half to more than the total of all organisms in the samples from Area One.

The analysis of the contents of the stomachs of brown trout show that *Asellus* was a very important part of the diet, particularly in Area Two (Fig. 3). The data in Figure 3 are based on the numbers of each kind of organism and might be misleading due to differences in size of the different food organisms. Therefore the importance of *Asellus* in the diet was further tested by comparing the food items on the basis of volume for the month of April. The average volume of each kind of food organism in the stomach samples was derived from the values obtained for the same species in the April bottom samples.

Table 4 presents results of the numerical

and volumetric analysis of the stomach samples for April. From these data it is apparent that an evaluation of the role of the major food items on the basis of their numerical abundance minimizes the importance of *Asellus*. In Area One *Asellus* composed 21 per cent of the total number of organisms in the stomachs and contributed 48 per cent of the total volume. In Area Two the comparable figures were 56 per cent of the total number and 78 per cent of the total volume. It is probable that this difference in the results as based on the numerical as opposed to the volumetric importance of *Asellus* would be maintained or increased during the summer months due to the consumption of increasing numbers of the early instars of aquatic insects.

From a comparison of the results of the sampling of the bottom fauna (Table 3) and the contents of the stomachs collected from the same area the same month (Fig. 3) it is evident that the abundance of *Asellus* in the two types of samples were disproportionate. For example in April *Asellus* comprised 48 per cent of the volume of organisms in the stomachs from Area One and only 1 per cent of the volume of the bottom samples. The comparable figures for Area Two are 78 per cent in the stomachs and 20 per cent in the bottom samples. This wide divergence in the percentage of *Asellus* in the stomachs and bottom samples is present in all months sampled.

Information obtained indicated that either: (1) *Asellus* is more readily available to brown trout than are other food organisms, (2) it is preferred by brown trout, (3) sampling methods did not give a reliable index of its relative abundance, or (4) a combination of these factors.

Frost (1939) noted that in the River Rye, where an abundance of *Asellus aquaticus* occurred, brown trout fed to a great extent on this animal; but in the River Liffey where *Asellus* was common but not abundant, it was of little importance as a trout food. Frost concluded that in the River Liffey trout preferred the larval forms of aquatic insects to the crustaceans, *Asellus* and *Gammarus*. Results at Houghton Creek seem to indicate that brown trout

preferred *Asellus* and *Gammarus* over the aquatic insects (Fig. 3).

During July and August, and probably most of June, Area One was characterized by a paucity of food. At this time of year abundance of bottom fauna was at its minimum, trout in Area One fed extensively on terrestrial foods, and the number of organisms per stomach was sharply reduced (Fig. 3). Fewer organisms per stomach during late summer has been observed for brown trout (Neill 1938, and Frost 1939), brook trout (Benson 1954), and salmon smolt (Allen 1940). None of these investigators attempted to correlate abundance of bottom food with numbers (or volume) of organisms per stomach. Surber (1936) found that rainbow trout from a stream with no shortage of aquatic food switched to terrestrial foods in midsummer.

Our belief is that in Area One of Houghton Creek the change to a diet consisting of a considerable proportion of terrestrial organisms, the reduction in the quantity of food per stomach, and the sharp drop in condition were all due to a paucity of food of aquatic origin. The belief is substantiated when the data from the two areas are compared in regard to the volume of bottom fauna available, amount of food in the stomach samples, the use of terrestrial animals as food, and the changes in the coefficient of condition of trout. More bottom food was available in Area Two at all times, stomach samples from this area contained more food during the summer months and did not show the sharp increase in numbers of terrestrial organisms observed in Area One, and the coefficient of condition of the fish of Area Two was significantly higher and much less variable than in Area One.

The contrast between the growth of the two groups of fish, as expressed by coefficient of condition, does not support Brown's (1946a) hypothesis of an intrinsic physiological growth cycle during that part of the year when temperatures are suitable for growth. These findings indicate that growth at this season is strongly influenced by the quantity and kinds of food available. An important difference in the food supply

of these two areas was the comparative stability of a crustacean food source as contrasted to the marked seasonal fluctuation in abundance of insect food. The importance of the type of animal food present is further emphasized by the evidence that brown trout ate crustacean food even when it may have been less abundant than aquatic insects.

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The Significance of Variations in the Strontium Content of Deep Sea Cores

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ABSTRACT

An Atlantic equatorial eupelagic core, Lamont A180-76, was systematically analyzed for strontium and calcium at 10-cm intervals down the core. The globigerina contribution to the core was found to contain essentially a constant strontium-to-calcium ratio independent of depth in the core. When the globigerina contribution to the strontium and calcium contents of the core are subtracted, a variation in the strontium-to-calcium ratio for the fine fraction is observed which is related to the Ericson temperature curve for the core—the high strontium-to-calcium ratio corresponding to a time of high surface ocean temperature. It is postulated that this sympathetic variation is best explained as the representation of the relative abundance of celestite tests secreted by an acantharian radiolaria. If the carbonate and lutite sedimentation rates are sensibly constant, then *Acantharia* productivity is temperature dependent. On the other hand, recent work has shown that the rate of sedimentation in the Atlantic equatorial region during the last glacial period was twice as high as the present rate. Since the strontium-to-calcium ratio of the fine fraction is roughly half as great for glacial time relative to recent times, this may be interpreted as the expression of a constant rate of celestite deposition.

INTRODUCTION

The recent preliminary examination of the strontium-to-calcium ratio variation with depth in a eupelagic deep sea core by Turekian and Kulp (1956) indicated significant differences between the various levels sampled. In addition, the average strontium-to-calcium ratio for the core as a whole was significantly lower than the values reported previously by Kulp, Turekian, and Boyd (1952) for three Atlantic cores of Tertiary age. Other data on deep sea cores and globigerina tests (Odum 1950, Emiliani 1955, Thompson and Chow 1956) generally indicated lower values than those reported in the above two papers by the writer. The several analyses are compared in Table 1. Since the various investigators were able to reproduce data on similar samples other than the specific materials under discussion, it was felt that the differences were probably significant and that an interesting problem lay in the apparent discrepancies observed.

Consequently a systematic study on the distribution of strontium in another eupelagic core was made. These results, together with the above-mentioned analyses, provide the framework for evaluating the

significance of variations in the strontium-to-calcium ratio of deep sea cores.

EXPERIMENTAL METHODS

A single Atlantic equatorial eupelagic core, A180-76 (for description see Ericson and Wollin 1956) was sampled every 10 cm down its length. On each segment the per cent coarse fraction (>74 micron) had been determined by Ericson and Wollin (1956). In addition, the total calcium carbonate contribution to the segment was determined by the technique described by Turekian (1956). Figure 1 taken from that paper shows the variation in the calcium carbonate content of the core and its relation to the $>74\mu$ fraction. It is to be noted that core A180-76 is essentially a high calcium carbonate core. Each entire segment was then analyzed for the strontium content using an emission spectrographic technique described previously (Kulp, Turekian, and Boyd 1952; Turekian, Gast, and Kulp 1957).

Figure 2 shows the variation in the strontium-to-calcium ratio observed with depth in the core. For the core as a whole the variation is great but no simple correlation with temperature, carbonate content, or

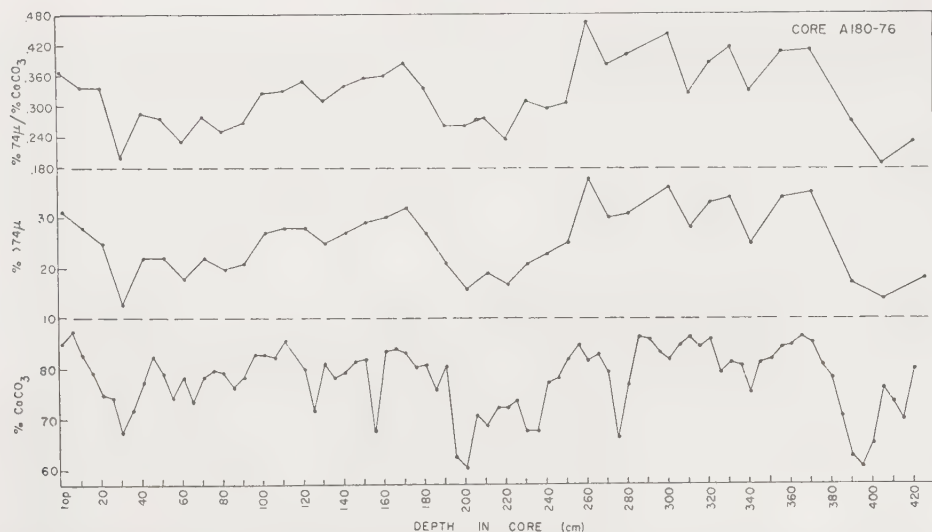


FIG. 1. Variation in carbonate content down a deep-sea core, Lamont A180-76, sampled at 5-cm intervals, compared with the "greater-than-74-micron" fraction (containing mainly globigerina tests). Data obtained by technique described in Turekian (1956).

any other investigated parameter is immediately apparent.

DISCUSSION

The effect of the globigerina contribution

It was thought that a subdued temperature effect might be present in the amount of strontium that the main identifiable calcium carbonate contributor, globigerina, could take up. This would be analogous to the increase of strontium with temperature in the Serpulidae as reported by Lowenstam (1954). Of course, in this case the increase in strontium was attributable to the increase in the aragonite-to-calcite ratio with increasing temperature. Kulp, Turekian, and Boyd (1952) and Odum (1950) have reported no measurable effect on the strontium content of shells as a result of temperature, provided either aragonitic or calcitic tests only are deposited. The possibility of a temperature dependence was initially entertained for globigerina because of the discrepancy observed between the very high strontium values reported by Kulp, Turekian, and Boyd (1952) for Tertiary deep sea "globigerina ooze" and the low value reported by Odum (1950) on Pleistocene cores (see Table 1). Emiliani (1955) and Thompson and Chow (1956) also report low values for globigerina in-

consistent with the data of Kulp, Turekian, and Boyd (1952).

Recent re-identifications of the particular cores analyzed by Kulp, Turekian, and Boyd (1952) show that these Tertiary cores, though high in calcium carbonate, have very few globigerina tests present. Hence their analyses of the cores do not represent the strontium-to-calcium ratio of globigerina.

This was confirmed by analyzing separated globigerina tests from core A180-76 at several different levels. Table 2 lists the values obtained. It will be seen that globigerina ooze is monotonously low at a value of 2.8 ($\%Sr/\%Ca \times 10^3$). This is consistent with the same more or less constant value reported by Emiliani (1955) for separated globigerina tests from the Atlantic, Pacific, and Caribbean. Thompson and Chow (1956) report a value of 3.3 which is also in good agreement.

The effect of the less-than-74-micron fraction

If the >74 -micron fraction is assumed to contain most of the globigerina tests, then it is possible to subtract the contribution of this type of organism to the strontium content of the core. This approximation will provide the lowest possible value of the strontium-to-calcium ratio to be ascribed to the non-globigerina contribution to the core. Plotting the $\%Sr/\%Ca \times 10^3$ ratio for the

CORE A 180-76

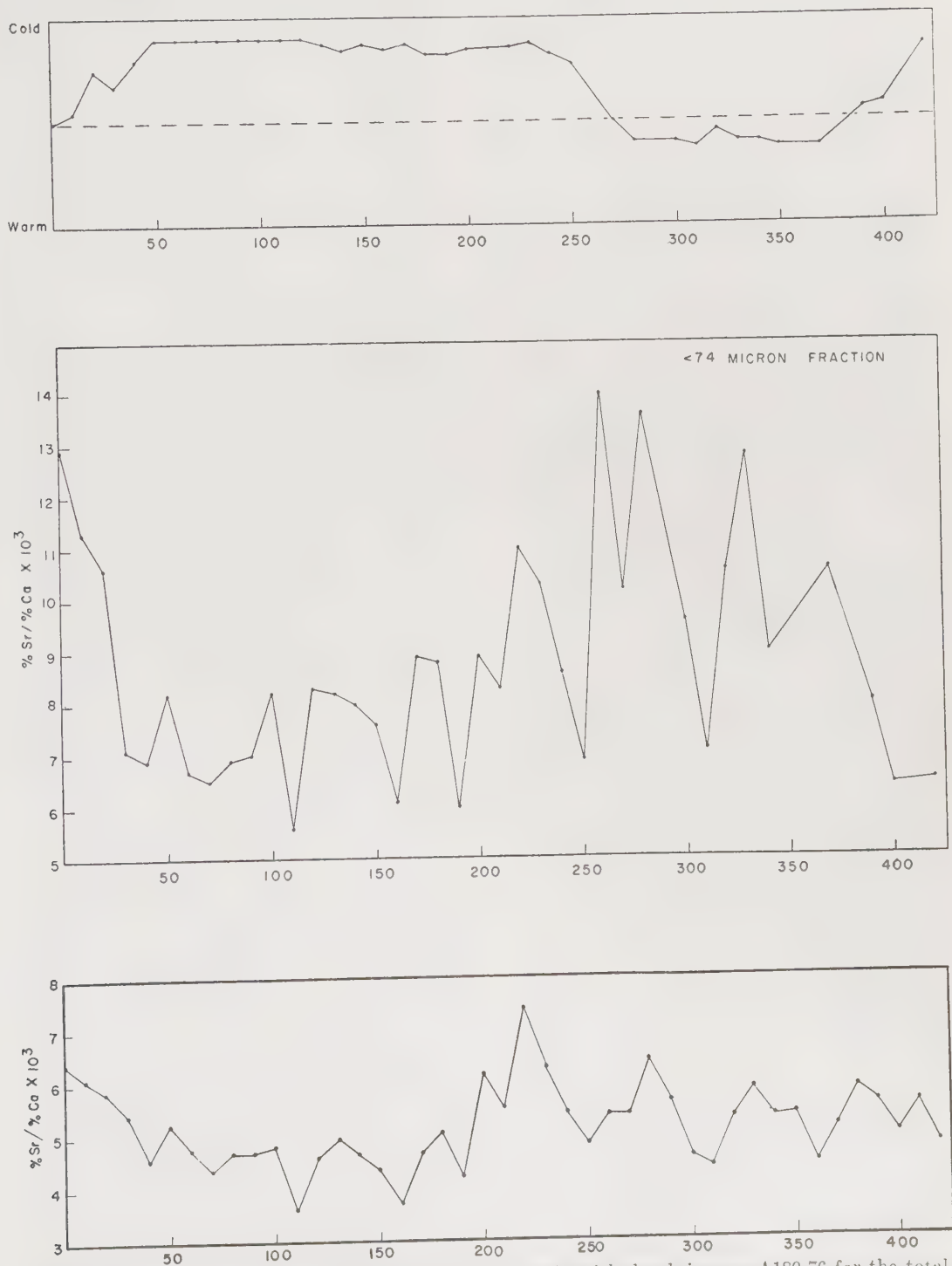


FIG. 2. The variation of the strontium-to-calcium ratio with depth in core A180-76 for the total core and < 74-micron fraction. The top curve is the comparable temperature curve taken from Ericson and Wollin (1956).

TABLE 1. *Strontium-to-calcium ratios reported for deep-sea cores and globigerina tests*

Reference	Description	%Sr/%Ca × 10 ³
Odum (1950)	"globigerina ooze"	5.5-6.6
	"foraminiferal ooze" surface-1000 m; average of 4	5.7
	"foraminiferal ooze" 1000-3400 m; average of 8	3.3
	Core A167-21: Upper Eocene	~24.0
Kulp, Turekian, and Boyd (1952)	Core A167-22: Oligocene	~20.0
	Core A167-29: Upper Miocene	~20.0
Emiliani (1955)	Average of separated globigerina tests	2.8
Thompson and Chow (1956)	"Deep sea sediments," Indian Ocean	4.2
	"globigerina ooze," Pacific Ocean	3.3
Turekian and Kulp (1956)	Core A180-74 (average value)	5.9

TABLE 2. *Strontium content of globigerina tests from Core A180-76 and other sources*

Depth in core (cm)	%Sr/% Ca × 10 ³
top	2.8
100	2.8
200	2.8
400	2.8
Emiliani (1955)	2.8
Thompson and Chow (1956)	3.3
Odum (1950)	3.7

less-than-74-micron fraction of core material (siliceous lutite and carbonate—though the siliceous lutite fraction contains very little of the calcium or strontium) we observe in Figure 2 that there are: (1) some very high values of the strontium-to-calcium ratio which are greater than that for most common calcium-carbonate-depositing organisms and which approach the value of sea water (Odum 1951), and (2) a systematic variation in this ratio with the temperature curve obtained by Ericson and Wollin (1956), the high strontium-to-calcium ratio corresponding to a high temperature of the ocean surface.

Possible causes for the variation in the less-than-74-micron fraction

The variation in the strontium-to-calcium ratio in the less-than-74-micron fraction being correlatable to variations in the surface temperature of the oceans and hence to the glacial and interglacial periods suggests that any source for the strontium must itself be a function of the sedimentation

TABLE 3. *Analyses of planktonic ash from a wide range of stations in the North Atlantic*

	%Mg/%Ca	%Sr/%Ca × 10 ³
SF 3	0.363	21.8
SF 4	0.510	22.3
SF 5	0.266	16.7
SF 6	0.316	14.4
SF 7	0.312	15.0
SF 8	0.182	10.1
SF 9	0.100	8.6
SF 10	0.239	26.3
SF 11	0.269	30.0
SF 12	0.471	12.0

pattern resulting from these major changes in the ocean. Three alternatives present themselves: (1) the varying contribution and hence temperature dependence of undifferentiated planktonic material, (2) the varying composition of glacial and non-glacial siliceous lutite, and (3) the varying contribution of tests made up of very high strontium content, specifically celestite (strontium sulfate) tests, with a change in surface water temperature. Of these choices, the last one seems the most probable for a variety of reasons to be discussed.

Undifferentiated planktonic material.

Table 3 presents data on the ash of planktonic material from a variety of stations in North Atlantic. The table gives the magnesium-to-calcium ratio as well as the strontium-to-calcium ratio for each sample. Some of the values of the strontium-to-calcium ratio are high, and if these organisms contributed directly to the sediment, then undoubtedly their varying productivity should be expressed as a significant variation in the strontium-to-calcium ratio for the sediment.

The magnesium-to-calcium ratio is also high for the ash, however, and the data from deep sea cores indicate that the total magnesium content, independent of the siliceous lutite contribution, is very much smaller than any of the ratios given in Table 3. Undoubtedly these ashes of planktonic material are high in both the strontium-to-calcium ratio and the magnesium-to-calcium ratio because of material included in cell material and in chitinous tests. Most of this material will not reach the bottom of the ocean.

Siliceous lutite fraction. A second possibility for the observed variation is that the siliceous lutite fraction during glacial times was higher in the strontium-to-calcium ratio by a considerable factor over present-day lutite. This is barely conceivable even if the lutite contribution during the glacial period was derived exclusively from high-alkali, low-calcium granites in which the ratio of $\%Sr/\%Ca \times 10^3$ is about 20 (Turekian and Kulp 1956) while the non-glacial period lutite source was considerably lower. This hypothesis is rejected on the evidence that the lutite fraction is generally free of both calcium and strontium. There is also no reason to believe that the lutite fraction, composed of authigenic clay minerals, should vary in the strontium-to-calcium ratio unless the oceanic medium itself had changed in composition. This change should also be recorded in the calcium carbonate fraction since Odum (1951) has shown a dependence of the strontium-to-calcium ratio of a shell on that of the water from which it is deposited. Table 2 shows that this is not the case for globigerina tests deposited during glacial and non-glacial times; hence we conclude that the source of the strontium variation lies elsewhere.

Acantharia contribution. As the last and preferred hypothesis it is proposed that the high values of strontium are the representation of the increased relative productivity of an organism with a strontium-rich test. Since most calcium-carbonate-secreting organisms do not have ratios of strontium to calcium to account for the high values noted, it is not probable that variations in the relative abundances of different species of calcium carbonate organisms can be responsible for the effect. Neither can variations in the strontium uptake of a single species be considered. Only the worm family Serpulidae and some continental shelf mollusks have the capacity to vary their strontium content with temperature, and despite the reported high value of strontium for warm water Serpulidae, it is not conceivable that their presence could account for the observed variations.

It seems probable then that the variation

in the strontium-to-calcium ratio with temperature is due to the relative supply of strontium sulfate (celestite) tests. There is good evidence, recently confirmed by Odum (1951), for the celestite composition of the test of a radiolarian, *Acantharia*. These radiolaria are present in the North Atlantic at the present time. Hence it appears that the deep sea cores record temperature changes as reflected by the variable relative abundance of celestite deposited by *Acantharia* or some similar organism.

This throws new light on the values obtained by Kulp, Turekian, and Boyd (1952) which indicate very high strontium-to-calcium ratios for several epochs of the Tertiary (Table 1). These sediments record a high ratio, possibly as a consequence of the relatively great abundance of celestite depositing organisms. If this is a measure of the relative temperature of the oceans, it indicates that the Tertiary oceans were at least as warm as, if not warmer than, the present-day seas. This seems to have been demonstrated by Emiliani (1954) for Pacific abyssal waters by means of oxygen isotope temperature determinations on benthic foraminifera.

Relation to rate of sedimentation in the deep sea

In the above discussion it was carefully noted that the high strontium-to-calcium ratio during the warmer or non-glacial periods possibly represented a higher *relative* productivity of *Acantharia* when compared to the carbonate productivity. It may have seemed that it was implied that the controlling factor was the increased or decreased productivity of the celestite tests while the calcium carbonate productivity remained essentially constant. This is probably not the case.

Recent work at the Lamont Geological Observatory and at Yale (Broecker, Turekian, and Heezen, in preparation) indicates that for the Atlantic equatorial region, from which core A180-76 was taken, the rate of calcium carbonate sedimentation was *twice* as great during the time of the last glaciation as at present. The same holds true for the siliceous lutite fraction. It is to be noted

that the strontium-to-calcium ratio for the less-than-74-micron fraction of the recent warm period is *about twice* that of the ratio during the glacial period.

If this is a significant correlation it indicates that the celestite fraction is essentially being deposited at a constant rate and the lutite and carbonate fractions are varying. This appears to be the same for the observable globigerina contribution (Fig. 1) and implies that the varying carbonate content is due to some variable oceanic condition which maintains a constant rate of globigerina and celestite accumulation but a varying *fine fraction* carbonate accumulation. This matter is discussed more thoroughly in the paper by Broecker, Turekian, and Heezen now in preparation.

SUMMARY

1. An Atlantic equatorial eupelagic deep sea core, A180-76, was systematically analyzed for strontium and calcium at 10-cm intervals down the length of the core. A significant variation in the strontium to calcium ratio was observed.

2. The globigerina contribution of the core was found to contain essentially a constant strontium-to-calcium ratio independent of location in the core.

3. Using the data on the greater-than-74-micron fraction of each segment of the core and assuming that most of the globigerina contribution is to be found in this fraction, it was possible to evaluate the strontium-to-calcium ratio of the fine grained material of the core. This showed a variation which was relatable to the surface ocean temperature as measured by Ericson and Wollin.

4. Since it is shown that the sympathetic variations in the strontium-to-calcium ratio with surface ocean temperatures cannot be accounted quantitatively by variations in the contribution of "undifferentiated planktonic material" nor reasonably by variations in the chemical composition of the siliceous lutite fraction, it is postulated that it is a representation of the relative productivity of a celestite depositing radiolarian, *Acantharia*.

5. The high strontium-to-calcium values can then be related to a high productivity of

Acantharia during times of high surface ocean temperatures (whether during the interglacial periods or in the non-glaciated Tertiary) impressed on a constant calcium carbonate contribution.

6. Recent work indicates that the rate of sedimentation in the equatorial Atlantic was twice as great during the last glaciation as in the 10,000 years subsequent to it. Since the strontium-to-calcium ratio is reciprocally related by the same amount, an alternative to the last proposition may be that the celestite contribution has been depositing at a constant rate and that the variations observed are due to varying rates of calcium carbonate deposition.

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A Source of Phosphorus for the Western Basin of Lake Erie¹

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ABSTRACT

The western basin of Lake Erie is supplied with phosphate phosphorus by the Maumee River in Ohio. This is apparently the most important source for the lake due to the high phosphorus concentrations involved and the large volume of flow in the spring months. The phosphorus content of the river is affected by stream flow, local temperature, and effluent from the City of Toledo. The addition of phosphate phosphorus to Lake Erie by the Maumee River amounted to over 96 metric tons from June 1945 to May 1946. If the addition by the City of Toledo is included the total amount came to at least 125 metric tons in the same period.

There are essentially two ways in which nutrient materials are made available to lakes. One way constitutes a closed system in which there is a continuous cycle of uptake and release of nutrients that remain, for the most part, permanently within the lake and its basin. Such a system has been described by Hutchinson (1941). The other way of supplying nutrients is by an open system in which the materials are added to the lake by tributaries, surface runoff, and springs, take part in one or two seasonal cycles, and are then removed by either outflow or permanent retention in bottom sediments.

Pearsall (1923) attempted to show a rough temporal relationship between surface runoff, inorganic salts in lake water, and diatom maxima. Slack (1955) noted an increase in the phosphorus content of river water associated with increased river discharge. Although the relationship between physical and chemical factors and the seasonal maxima of phytoplankton is quite complex and still obscure, the relation between surface runoff and presence of inorganic salts in lake water can be demonstrated. The contribution of phosphorus to lakes and its biological results has become the increasing concern of sanitarians and

water works engineers (Harvey and Bendizen 1953). The following paper presents data relating the presence of inorganic phosphorus to tributary streamflow into the western basin of Lake Erie. Chandler and Weeks (1945) have already described the seasonal cycle of nutrient salts in this region, and correlated the presence of inorganic nitrogen in the lake with tributary stream flow, particular that of the Maumee.

METHODS

The dissolved inorganic phosphorus content of the Maumee River, Ohio, was determined at a "Bay" station, located at the river's mouth, and at a "Bridge" station, located just above the center of the City of Toledo (Fig. 1), in 1945 and 1946. These determinations were made by personnel of the Department of Chemistry of the University of Toledo at the request of the F. T. Stone Institute of Hydrobiology, and the data were made available to the author. The ammonium molybdate-stannous chloride method (American Public Health Association 1946, p. 80) was used. This method detects orthophosphate. The phosphorus in polyphosphate detergents, such as sodium hexametaphosphate, $(\text{NaPO}_3)_6$, is detected by this method to a limited extent (about 15% of the total present).

The average precipitation over the entire drainage basin has been computed on a daily basis from reports of the following weather stations in Ohio: Defiance, Lindlay,

¹ The data for this study were obtained through the courtesy of Dr. Thomas H. Langlois, former Director of the Stone Institute.

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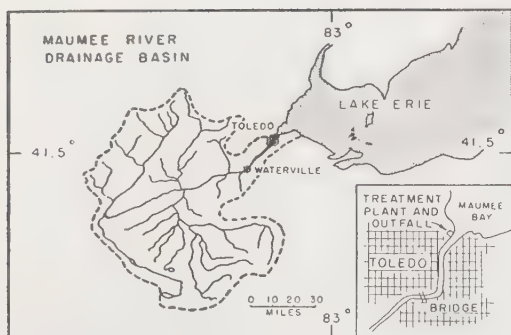


Fig. 1. Maumee River Drainage Basin.

Holgate, Lima, Montepelier, Ottawa, Van Wert, and Wauseon (U. S. Weather Bureau 1945-1946). The temperature data are averages of the maximum and minimum daily temperatures at Paulding and Toledo, Ohio (U. S. Weather Bureau 1945-1946). Discharge data are taken from Surface Water Supply papers (U. S. Geological Survey 1945-1946). The gauging station was located at Waterville, Ohio, seven miles upstream from Toledo.

DESCRIPTION OF THE MAUMEE RIVER DRAINAGE BASIN

(Largely from Cross and Bernhagen 1949)

The St. Marys and St. Joseph Rivers join to form the Maumee River at Fort Wayne, Indiana (Fig. 1). The Maumee drains 6,586 square miles and is the second largest river flowing into the western basin of Lake Erie, accounting for 2.4% of the total tributary flow. The largest tributary is the Detroit River which accounts for 96.7% of the flow. A major portion of the drainage basin, particularly the central part, is quite flat. Bedrocks in the region have little direct influence on stream flow. There are few large deposits of permeable materials. Fine sand, silt, and clay predominate in the surficial deposits on the floor of ancient Lake Maumee.

Limey glacial soils prevail over the till plains that form the periphery of the basin. Drainage is very poor and the soils are heavy and impervious. This characteristic is reflected in the extremely low stream flows during drought.

OBSERVATIONS

Periods of high precipitation occurred in June, July, September, and December, 1945, and May, 1946. Secondary peaks of precipitation occurred in nearly all months of the year (Fig. 2).

The periods of high stream flow in the Maumee River occurred shortly after periods of moderate or high precipitation. The average monthly discharge of the river for a fifteen-year period is compared to the 1945-1946 data in Table 1. The period of greatest discharge occurs ordinarily in late winter and the spring. Comparison shows that 1945 and 1946 were average years with

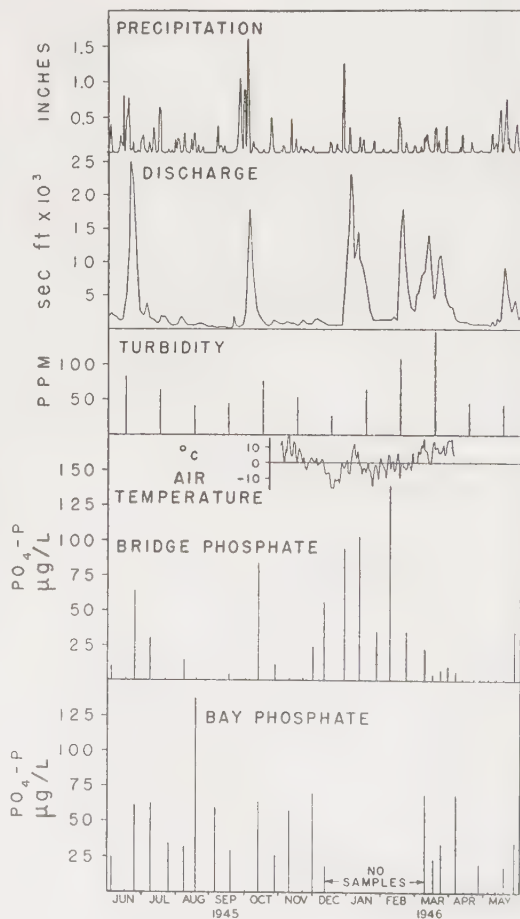


FIG. 2. Trends of average precipitation on Maumee River Basin, Maumee River discharge, turbidity, dissolved phosphorus at two stations, and air temperature.

TABLE 1. *Comparison of average discharge (in sec. ft.) of Maumee River at Waterville, Ohio (1931-1947) with discharge in 1945-1946*

Month	15-yr average	1945-1946
June	3640	7050
July	1680	1620
August	700	777
September	560	484
October	700	3856
November	1260	1015
December	2660	3174
January	4750	7491
February	4750	4724
March	9500	7876
April	8950	914
May	8100	2898

the exceptions of June, October, April, and May. In general, a wetter-than-average winter and a drier-than-average spring was experienced.

Stream flow was depressed during the intervals from December 1 to December 25, 1945, and from January 15 to February 10, 1946, when mean daily temperatures were below freezing 80% of the time (Fig. 2). The high river discharge in late December and early January occurred during a thaw and shortly after the fall of 1.3 inches of precipitation.

Monthly average turbidities ranged from 30 ppm to 150 ppm (diatomaceous earth standard). Turbidities reached their lowest values in December, concurrently with minimum winter temperatures (-10°C and less) and low discharge. Thereafter the turbidities increased to their highest point in March, during which time there was an upward trend in temperature.

High phosphorus concentrations were observed at the Bridge station within a few days following the June, 1945, peak discharge and within ten days following the October, 1945, peak discharge. From November, 1945, to February, 1946, the phosphorus concentration increased except for a low value observed in late January. This increase was not closely correlated with the increase in discharge during the same period. On February 7, there was an abrupt decrease in phosphorus level which was maintained

despite the subsequent periodic high rate of discharge. Low phosphorus values continued into May, when a slight increase was observed.

The average phosphorus concentration was higher at the Bay station than at the Bridge ($43\text{ }\mu\text{g PO}_4\text{-P/L}$ in the Bay compared to $25\text{ }\mu\text{g PO}_4\text{-P/L}$ in the river). At the Bay station there appears to be no relation between river discharge and phosphorus level. It will be noted that the datum points tend to fall on a high, medium, or low value without intermediate points. Winter samples are absent for the Bay no doubt due to the difficulties encountered in sampling.

DISCUSSION

Comparison of Bay and Bridge phosphorus

The Bay data exhibit one or more values over $50\text{ }\mu\text{g PO}_4\text{-P/L}$ in each month except May. The average phosphorus concentration at the Bridge is 58% of that at the Bay. Leaching of phosphorus from the suspended sediment in the Bay might account, in part, for the increase downstream. It is more probable, however, that the higher values reflect the influence of Toledo's domestic and industrial sewage. In only one case (October 12) does the phosphorus at the Bridge exceed that in the Bay. In the Bay data the values between 17 and $70\text{ }\mu\text{g PO}_4\text{-P/L}$ are apparently fluctuations around a fairly constant sewage load and depend upon dilution due to rainfall, etc. All the very low Bay values, $0\text{--}5\text{ }\mu\text{g PO}_4\text{-P/L}$, occur simultaneously with low values at the Bridge. The June 15 and September 30 low values are associated with peaks of precipitation and can be accounted for on the basis of local dilution by precipitation before phosphorus enriched water comes from upstream. The low values on November 19 are not associated with high precipitation, and phosphorus values at the Bridge were low on two preceding dates. These low values and the ones in April and May could possibly be due to initial low river phosphate plus the intrusion and mixing of low phosphate lake water in the Bay. Water of Detroit River origin has an

average phosphorus concentration of 2 $\mu\text{g PO}_4\text{-P/L}$ (author's data). This water frequently approaches the Maumee River estuary (Olson 1950).

Manner of phosphorus loss

Phosphorus is found in the soil in at least four forms: as mineral, free dissolved organic or inorganic form, particulate organic form, and adsorbed onto soil particles. When it is added to soil as phosphate it combines with ions in the soil solution to form one or more of the following: calcium, magnesium, iron, and aluminum phosphates, organic phosphates. Calcium phosphate is most readily available of these compounds to plants. Schollenberger (1920) has concluded that over thirty per cent of the total phosphorus in Ohio surface soils is in organic combination.

Truog (1948) discusses the availability of plant nutrients with regard to soil pH. At pH 6.5 or above there is sufficient CaCO_3 in the soil solution to keep a large part of the phosphorus as calcium phosphate which, being soluble in carbonic acid solution, is readily available in aerated soil or in the acid secretions of plants. As the pH increases to 8.5 or higher, sodium phosphate tends to develop, which is very soluble.

At a pH of 6 or less the concentration of $\text{Ca}(\text{HCO}_3)_2$ becomes less and the tendency to form $\text{Ca}_3(\text{PO}_4)_2$ is decreased. Increasing amounts of basic ferric phosphate are formed by combination with hydrated iron oxides. Combinations of phosphate with aluminum oxides and silicates also tends to increase with a drop in pH.

Olson (1928) has shown a range of soil pH of from 6.8 to 8.4 in the Maumee drainage basin, with an average of 7.8. No values lower than 6.5 were encountered, indicating, that the phosphorus in the soil was loosely bound.

On the basis of impervious soils and the presence of erosion conducive crops, *i.e.* 58% of the watershed in cultivation, 20% in corn in 1950 (Langlois, personal communication) it will be seen that the Maumee Valley presents ideal conditions for soil and water loss by runoff. Phosphorus can be leached out of the soil and transported

during erosion. The latter is necessarily a more rapid process and gives no opportunity for recapture of the phosphorus by base exchange.

The Maumee River frequently has turbidities up to 250 ppm (over 800 ppm with a diatomaceous earth standard). The high phosphorus values in December-February represents a 7.5-fold increase over the August-September period. During the same period stream discharge increased six times whereas turbidity increased only 2.5 times. Data on suspended matter in streams do not, therefore, indicate the loss of dissolved phosphorus. However, the total phosphorus loss is probably more closely correlated with turbidity values.

The increase in phosphorus level beginning in November, unaccompanied by a rise in discharge rate, may be best accounted for by a decrease in cover vegetation during the fall and increasing instability of the soil due to low temperatures. In addition, flowing water that would have entered the ground in warmer weather would move over a frozen soil surface during warm parts of the day and erosion would be increased. Such a condition could have persisted until continued sub-freezing temperatures slowed or stopped water movement for almost a month (February).

The highest phosphorus value (137 $\mu\text{g PO}_4\text{-P/L}$ on February 7) occurred five days before the corresponding discharge peak. It appears possible that the few warm days immediately preceding were enough to release a soil slurry with a high concentration of phosphorus.

The foregoing data indicate that increased surface runoff, whether due to precipitation directly or release of ground water, leads to greatly increased phosphorus concentrations per unit volume. Both the total amount and the concentration are increased during periods of high discharge. The significance of this result for phytoplankton production in river-fed bodies of water is obvious.

Statements such as, "Phosphorus in the soil is a very stable plant nutrient because it does not move from the place it is applied" (Anonymous 1947, p. 43), can be very misleading.

Pierre and Parker (1927) give 500 μg $\text{PO}_4\text{-P/L}$ as the highest concentrations of phosphorus to be found in the most fertile soils (in soil solution). The highest Bridge value was 138 μg $\text{PO}_4\text{-P/L}$ which is 28 % of the maximum soil value. The lowest values reflect low runoff, rather than infinite dilution.

The mean Bay value of 43 μg $\text{PO}_4\text{-P/L}$ is above the highest mean of western Lake Erie found by the author in 1950 (37 μg $\text{PO}_4\text{-P/L}$). The water in the central part of the western basin averages only 10 μg $\text{PO}_4\text{-P/L}$.

The total amount of dissolved phosphorus carried into Lake Erie by the Maumee River in 1945-46 has been calculated from the discharge figures and interpolated phosphorus values at the Bridge station (Table 2). This amounted to at least 96 metric tons. Sixty-eight per cent of the total was contributed in just two winter months, 44 % in January and 24 % in February. It may be assumed that the pattern of nutrient addition to the lake in 1945-1946, shown in Table 2, is a typical one since the associated monthly discharge figures for this period are considered to be fairly normal and farming practices have not significantly changed in the Maumee basin for many decades.

The same discharge rate for each month is used for both the Bridge and Bay calculations. The difference in dissolved phosphorus at the two stations represents the addition by the City of Toledo. For the months shown, this addition is relatively constant compared to the total addition. If the missing data for the winter months are comparable, then the average mean addition of soluble phosphorus is 2.4 metric tons per month from the city. The total dissolved phosphorus furnished the Bay from surface drainage and Toledo might approach 125 tons per year or be even greater.

The total amount of phosphorus furnished by the city must be greater, since some of the element is present in organic combination and as complex polyphosphates. Bogan (1956) contemplates that typical domestic sewage contains 4-6 mg P/L, mostly as

TABLE 2. *Total dissolved inorganic phosphorus, in kilograms, discharged by the Maumee River in 1945-1946*

Month	Bridge	Bay	Difference
June	10,875	14,325	3,450
July	1,813	5,140	3,327
August	325	3,119	2,794
September	94	1,190	1,096
October	7,290	8,450	1,160
November	271	3,479	3,208
December	7,609	—	—
January	43,243	—	—
February	22,932	—	—
March	7,130	—	—
April	213	2,410	2,197
May	1,812	4,160	2,348
Total	96,607	—	—
Average	—	—	2,448

polyphosphates, a variable fraction of this being removed by treatment plants. The City of Toledo was using primary treatment only in 1945-1946 according to Niles (1956). Such treatment removes about 2 % of the phosphorus.

If the population of Toledo in 1945 is taken as 300,000 and the per capita phosphorus output is taken as 5.4×10^{-4} metric tons per year (Rudolphs 1947), then the calculated discharge (minus 2 % removal by primary treatment) is 160 metric tons per year. This amount is 35 tons more than estimated from the present observations. Since the analytical method detects none of the organic phosphorus and about 15 % of the polyphosphates, the surplus is not unreasonable.

In order to compare sources of phosphorus, it is useful to compute the contribution on the basis of the area of the drainage basin. Unfortunately there are very few places where the total yearly contribution of dissolved phosphorus to lakes has been measured. Sayer (1947) has stated the contribution of phosphorus by agricultural runoff and seepage to the Madison, Wisconsin, lake region to be 72 kg phosphorus per square mile. Another report (Wisconsin Committee on Water Pollution 1949) gives the contribution to Lake Mendota, Wisconsin, as 7.4 kg per square mile in 1946 and 12.6 kg per square mile in 1947. Lake Mendota received the smallest addition of

nutrients of the four Madison lakes, according to this report. In comparison, the phosphorus contribution to Lake Erie via the Maumee River in 1945-1946 was at least 19 kg per square mile. If the Toledo contribution is subtracted, there remains 14.6 kg per square mile. Since the Lake Mendota drainage was largely non-urban, its supply is comparable to the Lake Erie-Maumee River supply. It will be noted, however, that the intensity of phosphorus addition in the Madison region, due largely to urban influence apparently is four times greater than in the Maumee drainage basin, with a population less than one-third as large.

While no causal relationship can be claimed, the fact that the spring phytoplankton bloom frequently commences in February in Lake Erie demonstrates that the high phosphorus input (concentration) at least comes at an appropriate time. Maumee River water is the only abundant, concentrated source of phosphorus for the western basin of Lake Erie. There are other rivers contributing phosphorus, but either in very dilute form (*e.g.*, the Detroit River) or at much lower rates (Huron and Raisin Rivers). Indeed, all the other rivers, excluding the Detroit, contribute less than 1.0% of the total discharge into the lake.

Despite the tremendous amount of phosphate-poor water added to the western basin by the Detroit River, there is apparently little large-scale mixing between the water masses originating from the Detroit River and the south shore streams (Langlois 1954, p. 339).

As these conditions are partially the result of human activities, they represent a case of artificially enhanced eutrophication. A process similar to the one described by Edmondson *et al.* (1956) appears to be operating in the western basin of Lake Erie, supplementing its natural eutrophy.

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The Internal Distribution Patterns of a Calanoid Copepod Population, and a Description of a Modified Clarke-Bumpus Plankton Sampler

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ABSTRACT

The internal distribution patterns of all the developmental stages of a *Diaptomus sicioides* population were studied by taking a large number of small samples of the same size. Use was made of a modified Clark-Bumpus plankton sampler constructed so that the volume of water filtered could be pre-set, and the behavior of this sampler was studied using a number 20 net. The data for the distribution patterns were obtained from fifty-one samples of 56.8 liters each, collected over a period of forty-five minutes. From these samples Fisher's coefficient of dispersion ($S^2/\bar{X}$), was computed and used as a measure of dispersion. With the exception of nauplius II it was found that all the immature stages and the adult males and females were infradisersed at the lower five-per cent level of significance. Nauplius II was randomly dispersed, and the eggs were found to be superdispersed. When the stages were lumped to form categories such as total nauplii or total copepodids, randomness or superdispersion was found. The dependence of $S^2/\bar{X}$ on sample size, number of samples, and population density was examined.

INTRODUCTION

In order to understand the nature of a population, and especially if population density is to be correctly measured, the type of distribution of the individuals within the population should be known. The internal distribution patterns of all the stages of a calanoid copepod population were examined by using a ratio called Fischer's coefficient of dispersion, $S^2/\bar{X}$, where S^2 is the variance and $\bar{X}$ is the mean of the population. In a Poisson distribution this ratio is equal to unity, and any departure of this ratio from unity is a measure of dispersion. This coefficient has been used by others as a measure of dispersion of plankters in the study of internal distribution patterns, but no attempt has previously been made to segregate and examine the dispersion of all the developmental stages in a calanoid population.

The distribution of different animal groups in the plankton has been studied from this point of view by Ricker (1937), Langford (1938), Tonolli (1949), and Barnes and Marshall (1951). Ricker, using a Juday closing net to examine the variability of catches of freshwater plankton in Cultus Lake, found that *Cyclops* and copepod nauplii were infradisersed, and *Epischura* and *Bosmina* randomly distributed, whereas

Daphnia was superdispersed. Langford, using a plankton trap in Lake Nipissing, extended this work by comparing the mean and variance of a number of hauls taken at one station as well as over an area. He found that *Diaptomus* and *Cyclops* and the nauplii and metanauplii were aggregated, while *Epischura*, *Daphnia*, and *Bosmina* could be considered as being distributed randomly. Tonolli using the Clarke-Bumpus plankton sampler tried to take samples of the same size by traversing the same measured distance each time, but he found this method to be unsatisfactory because the greater the population density the less the number of liters were filtered by the net. Also he suspected that the difference in density and viscosity of the water at different levels affected the number of liters filtered over the measured distance. Tonolli's work, which was based on triplicate samples of populations of *Diaptomus laciniatus* and *Diaptomus vulgaris*, showed two outstanding cases of infradisersion, *laciniatus* males at the surface and *vulgaris* males at 15 meters. In 93 series of comparisons infradisersion was found to be significant in only these two cases; however, he found superdispersion to be of frequent occurrence, particularly among the juvenile forms. Barnes and Marshall using a plankton

pump to get a large number of small samples found that in general when the population is low the distribution closely approaches the Poisson. At higher population densities the Neyman and Thomas series gives a better fit, indicating clumping of the organisms.

To make a study of internal distribution patterns it is necessary to take a large number of small samples of the same size. To avoid the difficulties encountered by Tonolli it was necessary to modify the Clarke-Bumpus sampler. In this paper the modified sampler and its calibration are described first, with a study of its behavior using a #20 net to take samples of a *Diaptomus oregonensis* population in Mary Lake, Itasca State Park, Minnesota. This is followed by a study of the internal distribution patterns of all the stages of a *Diaptomus siciloides* population in a lake in the Detroit Lakes region of Minnesota.

The authors are indebted to Prof. Douglas Chapman of the University of Washington who read this paper and offered valuable suggestions concerning some of the statistical treatments involved. Dr. David Gosslee, Statistician of the North Dakota Agricultural College Experiment Station, was consulted on several occasions with regard to treatment of the data, and we are very grateful for his advice. The conscientious efforts of Oscar Horner, Dorothy Tommerdahl, and George Sanderson in helping to take samples and counting them are gratefully acknowledged. Finally, we are also greatly indebted to J. T. Robertson of Fargo for his machine work in modifying the sampler. The field work on calibration of the sampler was done during the tenure of a National Science Foundation grant-in-aid at the Lake Itasca Forestry and Biological Station of the University of Minnesota, Itasca State Park, Minnesota. The remainder of the work was supported by Grant No. 1257 from the National Science Foundation, with additional support from the North Dakota Institute for Regional Studies. This paper is contribution number 9, Journal Series, from the North Dakota Institute for Regional Studies.

THE MODIFIED SAMPLER

Figure 1 shows the sampler with the mechanism for controlling the amount of water filtered. A detailed description of the construction and operation of the modification follows.

A vane *A* inside the housing directly drives a worm gear *B*, which in turn drives a pinion *C*, having ten teeth. This arrangement changes the direction of drive so that it is at right angles to the flow of water in the housing. The pinion *C* drives a second worm *D*, which again changes the direction of turning through a small gear *E* on a shaft *F* which lies above and parallel to the housing. This shaft turns a large geared wheel *G* by means of a second ten-tooth gear *H* which is fixed to shaft *F*. In turning, the large gear *G* eventually turns to a gap *Z* cut out at its periphery. When the large gear *G* turns until this gap is located over the small gear *H*, the large gear falls through a distance of about $\frac{1}{2}$ inch. This large gear *G* is mounted on a shaft *J* which has a right angle at its opposite end *K*, and the bent end is inserted into a hole drilled in the housing. Shaft *J* is constantly pressed away from the housing by means of a flat spring *L*, which is fastened to the housing surface by means of the same screws that mount the fin on that side of the sampler. The bent end of shaft *J*, which is $\frac{1}{2}$ inch long, projects inward toward the center of the housing and is long enough to act as a pin. The front gate is held open when this pin is set to hold the curved rod *O*, which is mounted on the gate at a right angle. The mechanism is ready to operate when the large geared wheel *G* is set in mesh with its driving pinion *H*. When the inside vane has turned an amount that brings the gap of the large wheel *G* over its driving gear *H*, the large wheel falls pulling the pin and releasing the front gate *P* so as to close it. The front gate itself is under tension to close by means of a spring *M*. A gate stop *N* is so mounted as to maintain the open gate parallel to the long axis of the housing. The gear sizes and tooth arrangement were chosen so that for every tooth moved on the large gear the inside vane turns ten turns. This arrangement makes it possible to control the

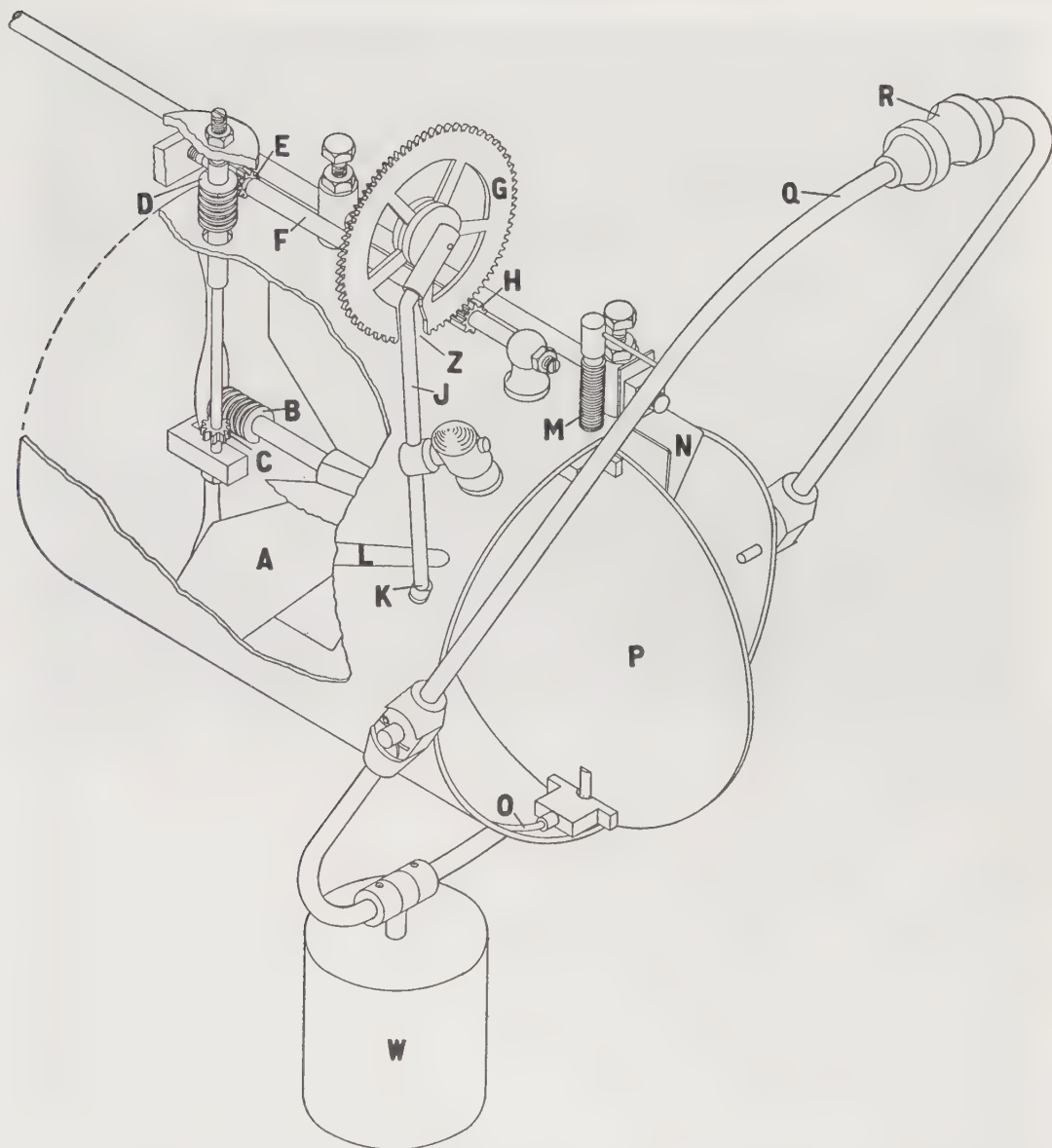


FIG. 1. Cut-away view of the modified Clark-Bumpus plankton sampler showing control mechanism that can be preset for passing through definite quantities of water. Lettering is explained in the text. Drawing was made by Frederick W. Stuve.

amount of water filtered simply by setting the large gear *G* shown in Figure 1.

The usual gate control mechanism found on the unmodified Clarke-Bumpus plankton sampler was removed entirely. In its place a simple brass loop *Q* was used. At the upper end a grooved spool *R* was added for attaching a cable or rope. At the lower end a three-pound lead weight *W* was attached

to stabilize the sampler during a tow and to aid in regulation of depth.

When taking small samples with this instrument, *i.e.* 50 revolutions or less, an appreciable jolt was experienced when the front gate closed, whereas when larger samples were taken the jolt was barely or not at all perceptible depending on sample size. The intensity of this jolt is apparently propor-



FIG. 2. Modified Clark-Bumpus plankton sampler mounted between influent and effluent cones. Water source is city water supply. Control of quantity of water passed is by valve as shown. Time required to fill the 55-gallon drum was used to compute the velocity.

tional to the flow of water through the sampler at the moment the gate closes. If the net is clogged the flow of water is so greatly decreased that the gate closes slowly and smoothly.

Calibration of the sampler

The method of calibrating the sampler was essentially the same as the "forced flume" method described by Yentsch and Duxbury (1956). Two steel cones (Fig. 2) were connected to the sampler so that one channelled water to it through a non-directional baffle from a water hydrant and the other conducted water away to a 55-gallon drum. The velocity of flow was computed from the time required to fill the drum.

Figure 3 demonstrates a straight-line relationship between revolutions per minute and liters per minute for volumes greater than 90 liters per minute measured as described above. The equation of this line, $y = 9.2 + 4.76x$, has been used to calculate

the volume of water filtered from the number of revolutions. This calibration equation gives results that are higher than those obtained by use of the constants of Yentsch and Duxbury from the "forced flume" method and the "modified flume" method; it yields results more comparable to those they obtained by the "measured water course" method. This may be due to differences in the samplers as well as methods of calibration, but it is more likely that it is due to the modification of the sampler.

According to Clarke and Bumpus (1950) the calibration should be done in water flowing at least $\frac{1}{2}$ knot or 40 revs/min (199.6 L/min), because somewhere below this the friction point is reached. Yentsch and Duxbury found that the friction point in their instruments was very close to the one published by Clarke and Bumpus. The data presented in Figure 3 illustrate that this sampler operated uniformly at a flow rate as low as $\frac{1}{4}$ knot or 20 revs/min (104.4 L/min).

It appears that this modified instrument has a different friction point as well as a different calibration value.

Behavior of the sampler in a lake

The sampler was used to take 25 plankton samples in Mary Lake, Itasca State Park, on August 17, 1954. Horizontal tows were made in many directions at a depth of approximately four feet. The tows were made at a velocity in excess of 2 knots, some error being due to the influence of the wind. The total time required to take the samples was about four hours, starting at 11 a.m. and ending at about 3 p.m.

All the samples were taken with a #20 net because the mean hole size of its meshes (0.07 mm) was considered to be fine enough to retain the stage I nauplii of calanoids. The length and some width measurements of the stage I nauplii of ten calanoids are listed in Table 1. It should be noted that the width measurements are of the body only, exclusive of the appendages; these measure-

TABLE 1. Median lengths and widths in millimeters of stage-I nauplii of ten species of calanoid copepods taken from preserved specimens

Where two measurements are shown, they represent a range: the smaller one is the size measured immediately upon emergence from the egg, the larger one is of a specimen apparently about to molt. Measurements are original with exceptions noted.

Copepod	Length	Width
<i>Diaptomus hesperus</i>	0.11-0.14	
<i>Diaptomus siciloides</i>	0.11-0.15	0.06-0.08
<i>Diaptomus ashlandi</i>	0.12	
<i>Diaptomus oregonensis</i>	0.13	
<i>Diaptomus sicilis</i>	0.15	
<i>Diaptomus gracilis</i> ¹	0.157	0.091
<i>Diaptomus vulgaris</i> ²	0.175	
<i>Diaptomus lacinatus</i> ¹	0.187	0.109
<i>Diaptomus castor</i> ²	0.19-0.2	0.10-0.11
<i>Limnocalanus johanseni</i>	0.2	

¹ measurements from Wuthrich 1948

² measurements from Gurney 1931

ments have been found to be 50 per cent or more of the length. While it appears that for the smaller species listed, such as those from *D. hesperus* to *D. sicilis* inclusive, the animals might go through the net, this would not be likely to occur because of the branching nature of the appendages.

In the Mary Lake samples the *Diaptomus oregonensis* population was in its copepodid stages of development; hence, the counts were necessarily made on copepodids. At the time of the study of the internal distribution patterns in Severson Lake, which contained a *Diaptomus siciloides* population, all the stages of the copepod were present.

The Mary Lake samples were taken in five series (Table 2). The first samples taken were those in Series I, in the following order: 20, 50, 100, 150, and 200 revolutions, the sampler being pre-set each time for the number of revolutions taken. The second and subsequent series were then taken similarly. The net was washed after each sample was taken.

It was found that clogging took place in each of the series and increased as the size of the sample increased. The relative amount of clogging during each of the hauls was noted by examining the length of time

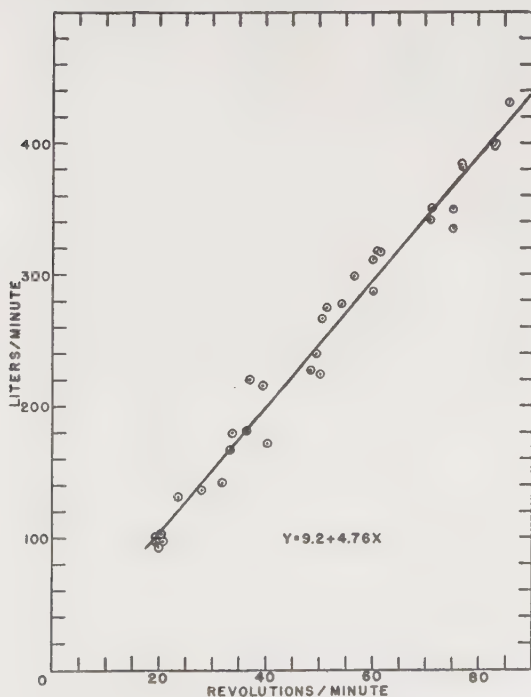


FIG. 3. Regression line of liters per minute as a function of revolutions per minute computed from data taken at water hydrant.

TABLE 2. Number of copepodids of *Diaptomus oregonensis* per sample

The series are numbered in the sequence in which they were taken. Mary Lake data.

Series	No. of Revolutions					Totals
	20	50	100	150	200	
1	4,042	8,314	21,733	24,791	28,114	86,994
2	4,843	8,334	18,267	24,166	29,200	84,810
3	2,892	6,334	13,567	18,041	23,450	64,293
4	1,313	3,034	9,367	12,459	16,791	42,964
5	3,879	6,134	15,767	19,125	21,041	65,946
Totals	16,969	32,150	78,701	98,582	118,605	

required to filter the five quantities of lake water. These times varied from 10 seconds for the 20-rev. samples to as much as 540 seconds (9 min) for the 200-rev. samples. The approximate time required to filter each of the five volumes does not follow the arithmetic multiple of the five volumes. Using the time required to take the 20-rev. volume as unity, if there were no clogging it should have required 25 seconds to take the 50-rev. volume; instead, 30 seconds were required. Fifty seconds should have been needed to take the 100-rev. volume instead of 100 seconds, 75 instead of 200 for the 150-rev. volume, and, finally, 26 to 54 times as much time was needed to take a sample that was only 10 times the volume of the 20-rev. sample. While these data are insufficient to warrant any conclusions concerning the rate of filtering, it is obvious that filtration decreases as the length of tow increases and the organisms concentrate in the net. If the net is clogged water can be forced through the net simply by prolonged towing.

The above data demonstrate that the smaller the sample taken the less the net becomes clogged. Yentsch and Duxbury have shown that the calibration constant of the sampler changes when the net becomes clogged. Therefore, under bloom conditions when the #20 net must be used the best estimate of the true population can be obtained by taking a number of small-size samples, because the calibration constant of the sampler is applicable only when the net is unclogged.

In order to compare the five series of data listed in Table 2 use was made of the analysis

TABLE 3. Analysis of covariance on Mary Lake data

The first hypothesis that the levels (α) and the slopes (β) of the five regression lines shown in Figure 4 are not significantly different was rejected at the 1% level, and the second hypothesis that only the slopes are not significantly different was not rejected at the 5% level.

Source of variation	Sum of squares	d.f.	Mean square
Total (S_T)	365,975,692.0	23	15,911,986.6
Within groups (S_E) or error	65,162,536.1	15	4,344,169.0
Between groups ($S_T - S_E$) or due to common regression	300,813,155.9	8	37,601,644.5

Hypothesis 1: $\alpha_1 = \alpha_2 = \alpha_3 = \alpha_4 = \alpha_5$ and $\beta_1 = \beta_2 = \beta_3 = \beta_4 = \beta_5$

$$F = \frac{S_T - S_E}{S_E} = 8.66$$

$$F_{.99} (8, 15) = 4.00$$

Since $F > 4.00$, reject Hypothesis 1.

Source of variation	Sum of squares	d.f.	Mean square
Total from regression lines with same slope (S_S)	103,574,361.9	19	5,451,282.2
Within groups (S_E) or error	65,162,536.1	15	4,344,169.0
Between groups ($S_S - S_E$) or due to common slope	38,411,825.8	4	9,602,956.4

Hypothesis 2: $\beta_1 = \beta_2 = \beta_3 = \beta_4 = \beta_5$

$$F = \frac{S_S - S_E}{S_E} = 2.21$$

$$F_{.95} (4, 15) = 3.06$$

Since $F < 3.06$, we cannot reject Hypothesis 2.

of covariance. For this test the x variable is the sample volume, and the y variable is the number of copepodids per sample. Since the number of copepodids per sample is used for the y variable, the calibration equation has not been used in the computations. In computing the regression lines for the analysis of covariance it was assumed that the number of animals taken was a linear function of the amount of water filtered only over the range studied so that the regression lines do not necessarily pass through the origin.

In Table 3 the results of the analysis of covariance are tabulated, and in Figure 4 the five regression lines from the data are plotted. The first hypothesis, that the five regression lines have both a common mean and a common slope, was rejected at the

1-per cent level. The second hypothesis, that the lines have a common slope, was not rejected at the 5-per cent level, which probably means that the x factor, volume of water, acts equally on all populations although at different numerical levels. It is possible that the slopes are different and that the data are insufficient to detect the differences; however, if the slopes are the same as indicated by the test, the levels of the lines must be different since the first hypothesis was rejected. The different levels for the five series of samples taken presumably reflects differences in density of the plankton in different parts of the lake.

APPLICATION OF THE MODIFIED SAMPLER TO THE STUDY OF INTERNAL DISTRIBUTION PATTERNS

With the modified Clarke-Bumpus plankton sampler 51 samples of the same size (56.8 liters = 10 revs.) were taken. A 10-rev. sample was considered to be small enough to minimize the clogging of the #20 net, which was again used in order to take all the stages of the life cycle. These samples were taken by dropping the instrument vertically to the bottom of the lake, generally less than 16 feet, and towing it to the surface by pulling it diagonally. The length of the tow was such that the sampler closed before it approached the surface of the lake.

The study was made in a small shallow lake (locally called Severson Lake or Olson Lake but otherwise without established name), maximum depth 16 feet, in the Detroit Lakes area in Minnesota on 27 July 1955. The time required to take all the samples was 45 minutes, from 10 to 10:45 a.m.

All stages of *Diaptomus siciloides* were counted in five 1-ml aliquots from each sample, and the mean for each stage taken. From these data the mean ($\bar{X}$) and the variance (S^2) of the 51 replicate hauls were computed for nauplius stages I, II, III, IV, V, and VI, copepodid stages I, II, III, IV, male and female V, male and female (ovigerous and nonovigerous) VI, and attached and unattached eggs.

The coefficient of dispersion for each of these stages was computed by dividing the variance by the mean, $S^2/\bar{X}$. With the simplest distribution, the Poisson, the coefficient is equal to one. When such a condition occurs the animals are considered to be randomly dispersed. The departure of this ratio from unity is used as a measure of dispersion. Where the variance is much greater than the mean, the coefficient is greater than one, and the organisms are grouped more than would be expected on the simple random hypothesis; this is known as superdispersion. Where the variance is much less than the mean, the coefficient is less than one, and the population is much more evenly spaced than in a randomly distributed one: this is known as infradisersion. The significance of deviations of $S^2/\bar{X}$ from unity, can be tested according to the equation: $\chi^2 = (n - 1) S^2/\bar{X}$, where n is the number of samples.

Interpretation of the internal distribution patterns

In Figure 5 a histogram of the coefficients of dispersion for all the categories is shown, the y -axis being logarithmic. The lightly dotted lines represent the 1- and 99-per cent

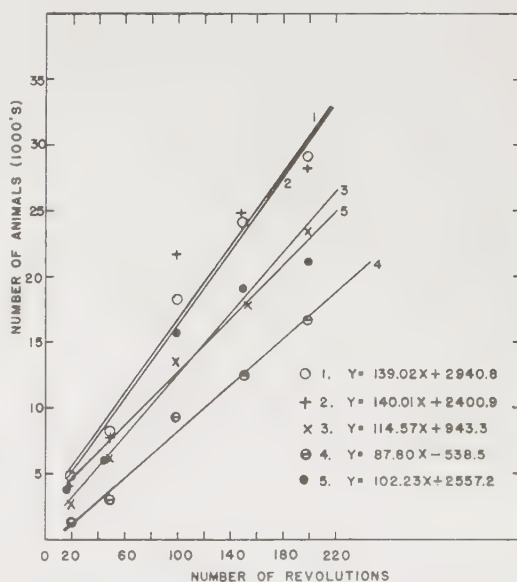


FIG. 4. Regression lines for the five series of data computed in the analysis of covariance.

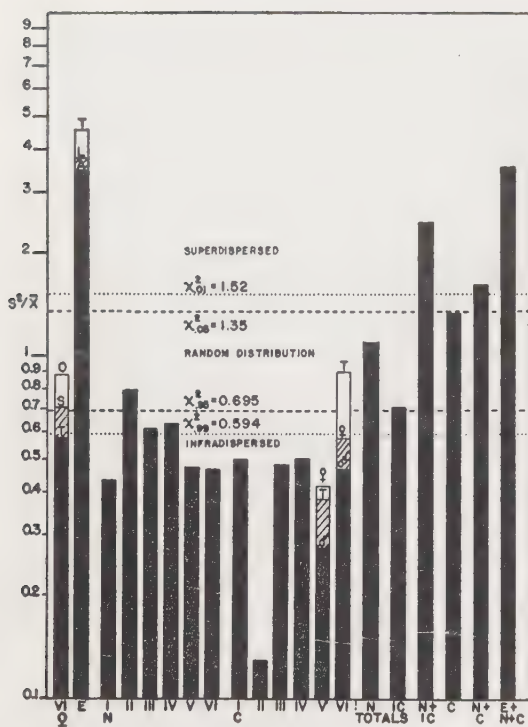


FIG. 5. Histogram of the coefficients of dispersion for the following categories: VI ♀, adult females; O, ovigerous females; S, nonovigerous females; T, total for the particular category; E, eggs; L, loose or unattached eggs; A, attached eggs; N-I, II, III, IV, V, VI, nauplius stages; C-I, II, III, IV, V, VI, copepodid stages; N, total nauplii; IC, total immature copepodids; N + IC, total nauplii and total immature copepodids; C, total copepodids; N + C, total nauplii + copepodids; E + N + C, total eggs + nauplii + copepodids. The y-axis is logarithmic. The lightly dotted lines are the 1% and 99% levels of significance. The heavily dotted lines are the 5% and 95% levels of significance.

levels of significance; the heavily dotted lines represent the 5- and 95-per cent levels of significance. Where the bars shown project above the 1- or 5-per cent levels, the population is superdispersed or clumped, and where the bars project to some point between the lines shown, the population is randomly dispersed; below the 95- or 99-per cent levels the population is infradispersed or more uniformly spaced than random.

The eggs were the most superdispersed of the components studied in the plankton, and when counted they were segregated into two categories: loose eggs and eggs attached to

the females. The superdispersion of the attached eggs is to be expected because they occur in clusters when attached to the female. Females with these eggs were found to be randomly distributed. Therefore, the distribution of the attached eggs can be said to be random clumped. The superdispersion of the loose eggs might be an indication that the pattern of the eggs was not disturbed significantly by external factors such as currents or gravity upon being released, presumably because the eggs do not exist for very long before hatching occurs.

The negative binomial distribution was found to fit both the attached and the unattached eggs (Table 4). This distribution is defined by two parameters, the mean and a positive exponent k , which was estimated by Fisher's method of maximum likelihood (Bliss and Fisher 1953). For the attached eggs the maximum likelihood estimate of $k = 2.0871$ and its variance $V_k = 0.4196$ were computed. For the unattached eggs k was found to be 5.2879 and $V_k = 1.268$. Table 4 shows that both populations can be accepted as fitting the negative binomial distribution at the 90-per cent level of significance. Also the frequency distribution for the attached eggs was fitted to Neyman's type A and Thomas' double Poisson distributions, by the methods given by Thomson (1952). The hypothesis that the attached eggs fit either of these distributions was rejected at the 99-per cent level of significance (Table 4).

Most of the immature stages, nauplii, and copepodids, were found to be infradispersed, with three exceptions to this at the lower 1-per cent level, N-II, N-III, and N-IV, and of these, N-III and N-IV are infradispersed at the lower 5-per cent level. Table 4 shows that N-II, N-III, and N-IV were found to fit the Poisson distribution at the 95-per cent level of significance, but only N-II could be accepted as fitting the Poisson at the 90-per cent level. Therefore, as a group the immature stages can probably be considered to be more uniformly spaced than random. This tendency toward uniform spacing is probably due to strong intraspecific competition for food or space or both. If the nauplii are considered collectively,

they are found to be randomly dispersed as are the immature copepodids when considered collectively. This indicates, therefore, that competition is less between stages where the size difference is greater than it is within a stage. This is substantiated by the fact that where all of the immature stages are considered collectively, so that an even greater size range is considered, they are found to be superdispersed. It seems probable that nauplii and copepodids occur in clumps because animals of different sizes coexist in micro-habitats where competition for food is not as strong due to feeding on different size particles, which has been found for some copepods (Lowndes 1935, Burckhardt 1935). In Tonolli's study all of the immature stages were lumped, and they were found to be superdispersed at all the lake levels studied (0, 5, 10, 15, 20, 30, 40, and 50 m). This is in agreement with the results obtained from our data by lumping stages.

When the stage-V copepodids are examined collectively they are infradispersed, and even when the sexes are separated they are still more uniformly spaced than random. If the mature or adult stages are examined in the same manner they are found to be random when the two sexes are considered collectively, whereas when they are separated they are infradispersed. This may indicate that the adult stages have a more complicated behavior than the stage-V copepodids. Since they are sexually mature their distribution pattern might be expected to be different because not only competition for food but also sexual attraction would influence their behavior. Competition for food tends to produce uniform spacing, which is indicated by the infradisersion found when the sexes are considered separately. Sexual attraction has the opposite effect, which is shown by the random dispersion found when the adults are considered collectively.

It should be noted that the adult females were separated into two categories: ovigerous and non-ovigerous. These two categories were infradispersed when considered collectively, but separately each was found to be randomly dispersed. This is to be expected since the bearing of eggs at any one

TABLE 4. *Goodness of fit of frequency distributions for indicated instars and lumped categories*

The nauplius II, total nauplius, total immature copepodids, non-ovigerous females, total adults, and total copepodids were found to fit the Poisson distribution at the 10% level of significance, nauplius III and IV and the ovigerous females at the 5% level. The attached and unattached eggs were found to fit the negative binomial distribution at the 10% level. The attached eggs were rejected as fitting Neyman's type A and Thomas' double Poisson distribution at the 1% level of significance.

Stage	d.f.	χ^2	$\chi^2_{.95}$	$\chi^2_{.90}$
Poisson distribution				
Nauplius II	5	8.40	11.07	9.24
Nauplius III	5	9.43	11.07	9.24
Nauplius IV	5	9.47	11.07	9.24
Total nauplius	5	4.46	11.07	9.24
Total immature copepodids	5	7.58	11.07	9.24
Non-ovigerous females	4	5.36	9.49	7.78
Ovigerous females	1	3.65	3.84	2.71
Total adults	5	7.37	11.07	9.24
Total copepodids	6	7.05	12.59	10.64
Negative binomial distribution				
Attached eggs	3	6.246	7.82	6.251
Unattached eggs	4	2.80	9.49	7.78
Neyman's Type A distribution				
Attached eggs	3	13.81	7.82	$\chi^2_{.99}$ 11.34
Thomas' double Poisson distribution, Method I				
Attached eggs	3	24.72	7.82	11.34

time would probably be a random process among the females.

The large number of cases of infradisersion found in this study are probably due to the fact that the stages of the animals were considered separately, since in agreement with the work of others many cases of superdispersion were found when stages were lumped. The segregation of the stages makes it more readily possible to determine the influence of the environment upon the distribution of the animals, since the variable of difference in development of the animals for the most part has been controlled.

EXAMINATION OF THE COEFFICIENT OF DISPERSION

Since the coefficient of dispersion was used extensively in plotting these data, it was

TABLE 5. *Comparison of distribution patterns when based upon 51 and 3 samples*

This table shows the change in type of internal distribution pattern as indicated by the coefficient of dispersion when the coefficient is computed from 51 samples as compared with the same computation based on 3 samples.

	Based on 51 samples	%	Based on 3 samples	%
Superdis- persed	6	22.2	0	0.0
Random	9	33.3	116	87.2
Infradispersed	12	44.4	17	12.8
Total	27	99.9	133	100.0

examined further with reference to three factors: number of samples taken, volume of samples filtered, and population density at the time of sampling.

The number of samples taken was found to have an effect on the coefficient of dispersion (Table 5). This was examined in five sets of three randomly selected samples from the 51 upon which this study is based. When only three samples are used, a marked predominance of random distributions occur. When 51 samples were used to determine $S^2/\bar{X}$, 33.3 per cent were found to be random, whereas when three samples were used this increased to 87.2 per cent. Again, based upon the 51 samples 22.2 per cent were superdispersed populations as against none based upon three samples, and similarly the infradisersed percentage decreased from 44.4 to 12.8. In view of these data, it is remarkable that Tonolli found a great many cases of superdispersion using only triplicate samples, but not at all surprising that no cases of infradisersion were found. It seems more likely, as mentioned previously, that lumping of the immature stages was responsible for his results since cases of superdispersion were found but none of infradisersion.

Ricker treated hypothetical data and showed that $S^2/\bar{X}$ remained constant upon changing the sample size, but experimentally it has been found to be influenced by sample size. Evans (1952) in a study on the influence of quadrat size on the distributional patterns of three plant populations

TABLE 6. *Coefficients of dispersion for different sample sizes based on the number of copepodids per sample from Mary Lake data*

$S^2/\bar{X}$ apparently bears no definite relation to sample size, and $S^2/\bar{X}^2$ decreases as sample size increases. Sample size is expressed as number of revolutions. $\bar{X}$ is the mean number of copepodids per sample computed from data in Table 2.

Sample size	$\bar{X}$	$S^2/\bar{X}$	$S^2/\bar{X}^2$
20	3,394	541	0.159
50	6,430	731	0.114
100	15,740	1,392	0.0884
150	19,716	1,285	0.0652
200	23,721	1,102	0.0465

found that the size of the quadrat affected all the measures of dispersion he investigated including $S^2/\bar{X}$. He found that when the quadrat size was doubled $S^2/\bar{X}$ increased, and that the differences between successive values of $S^2/\bar{X}$ was not directly proportional to the size of quadrat since they became greater with each increase in quadrat size. Our data also show that $S^2/\bar{X}$ is influenced by sample size. In Table 6 the coefficient of dispersion is listed for five different volumes. The data used are those from Mary Lake, the five samples taken at each volume being used as replicates. $S^2/\bar{X}$ was found to have no definite relationship to sample size although the values were affected by it.

Barnes and Marshall (1951) found that in general when the population was low the distribution was random, and at higher population densities superdispersion was usual. It appeared that our data varied in the same manner, and in order to examine this the population density was plotted against the coefficient of dispersion (Fig. 6). This graph indicates that there may be a linear relationship between the population density and the coefficient of dispersion. Three points representing egg populations in the lower right quadrant appear not to lie on the same line. Since the eggs are biologically very different from the other stages of the life cycle it is not surprising that they deviate considerably from the rest of the points. The correlation coefficient was computed for the two variables, $\bar{X}$ and

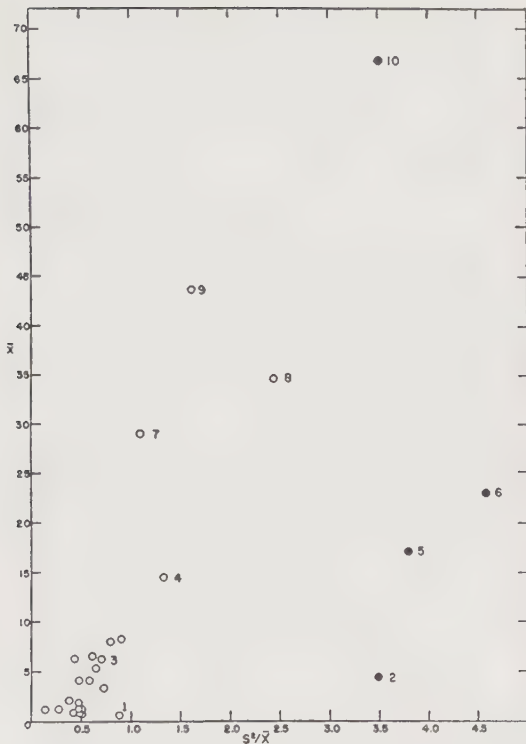


FIG. 6. The population density of Severson Lake (86.9 $\bar{X}$ is the mean number of animals per sample) plotted against Fisher's coefficient of dispersion for all the categories shown in Figure 5. The mean lake population is estimated to be 1530 $\bar{X}$ animals per cubic meter. Circle labelled 1 at bottom left represents the adult egg-bearing females; black dot 2 represents eggs attached to females; circle at 3, all the immature copepodids; 4, all the copepodids (including adults) lumped; 5, the loose eggs; 6, total eggs; 7, all the nauplius stages; 8, all the nauplii and immature copepodids; 9, all the nauplii and all the copepodids; 10, all the categories lumped: eggs, nauplii and copepodids.

$S^2/\bar{X}$, without the four points representing the eggs, and found to be 0.784, which was significantly different from zero at the 1-per cent level.

It might be supposed that by dividing $S^2/\bar{X}$ by $\bar{X}$ a statistic would be obtained which would be less dependent upon the population density than is $S^2/\bar{X}$. If the statistic $S^2/\bar{X}^2$ is calculated for the above data and the correlation coefficient recomputed for $\bar{X}$ and $S^2/\bar{X}^2$ for the same categories as above, the coefficient is -0.393 , which is not significantly different from zero at the 5-per cent level. However, it was found

that this statistic was also sensitive to sample size, decreasing as the sample size increased (Table 6).

SUMMARY

The Clarke-Bumpus plankton sampler has been modified so as to make it possible to take samples of the same size. The modification was such that the front gate on the sampler would close after a predetermined amount of water had passed through the instrument. The instrument was calibrated and the calibration equation was found to be $y = 9.2 + 4.76x$, where y is the number of liters filtered and x is the number of revolutions.

A *Diaptomus oregonensis* population was then sampled using a number 20 net in order to take all the nauplius stages. Five series of hauls were made, and in each series five different volumes were filtered: 20 revs. (104 liters), 50 revs. (247 liters), 100 revs. (485 liters), 150 revs. (723 liters), and 200 revs. (961 liters). The relative times required to take these samples showed that the net became progressively more clogged as the size of the samples increased. Since the calibration constant does not apply when the net is clogged, only the samples of small size could be used to estimate the population density.

The five series were then studied by an analysis of covariance. The first hypothesis that the five regression lines, the y -axis being the number of copepodids and the x -axis the number of revolutions, have a common mean and a common slope was rejected at the 1-per cent level. The second hypothesis that the lines have a common slope was not rejected at the 5-per cent level, which probably means that the x factor (volume of water) acts equally on all the populations although at different levels. The different levels for the five series of samples presumably reflect differences in density of the plankton in different parts of the lake.

With the modified instrument 51 samples of the same size were taken within a short period of time. From these samples a study was made of the internal distribution patterns of all stages of the life cycle of a *Diaptomus siciloides* population using Fish-

er's coefficient of dispersion, $S^2/\bar{X}$, where S^2 is the variance and $\bar{X}$ the mean of the population. All of the immature stages (Nauplius I, III, IV, V, VI, and Copepodid I, II, III, IV, V male, V female, and V total) and the adult males and females were found to be infradispersed at the lower 5-per cent level of significance except Nauplius II, which was found to fit the Poisson distribution. The total nauplius, total immature copepodids, ovigerous and non-ovigerous females, total adults, and total copepodids, were also found to fit the Poisson. The attached eggs and unattached eggs were superdispersed and found to fit the negative binomial distribution. Other superdispersed categories were only those that were lumped: the total nauplii and immature copepodids, total nauplii and copepodids and total eggs. The biological significance of these distributions is discussed.

An examination was made of the coefficient of dispersion with reference to population density, volume of sample, and number of samples. The coefficient was found to be dependent upon each of these factors.

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Daytime Variations in Phytoplankton Photosynthesis

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ABSTRACT

A study of CO₂-removal during July and August, 1954, under natural conditions in western Lake Erie demonstrated a maximal rate during the hours of 0700–1000 (10 μ moles CO₂ absorbed per liter of water per hour), a reduced rate during the hours 1000–1600 (6 μ mol/L/hr), a slightly negative rate during the daylight hours 1600–1900 (–1 μ mol/L/hr), and nighttime negative rates similar to the day-time positive rates (–6 μ mol/L/hr).

Doty and Oguri (1957) have reported evidence of daily periodicity in photosynthetic rates exhibited by marine phytoplankton. They demonstrated a 5.7-fold higher rate for collections taken at 0800 than for collections taken at 1900, and showed that a sharp decline in photosynthetic capacity was evident during the late daylight hours 1600–2000.

In my report on photosynthesis of phytoplankton in western Lake Erie (Verduin 1956a) I described a method of measuring photosynthesis under completely natural conditions. This is accomplished by measuring the pH of water samples collected at intervals during the day, using a Beckman pH meter. The pH change between any two intervals can then be converted to CO₂ change by referring to a curve prepared by differential titration of the lake water with 0.01N NaOH. During July and August, 1954, surface water pH values were determined at 3-hour intervals with the exception of the 2200–0700 interval, during which no determinations were made. These determinations were not planned to study periodicity in photosynthesis, but simply to measure the magnitude of CO₂ changes under completely natural conditions. After reading the paper by Doty and Oguri I recognized that our data contained an interesting trend which might represent the effect of this phenomenon. The observed pH changes during each time interval (Eastern Standard time) were converted to μ moles CO₂ absorbed per liter of water per hour and are shown in Figure 1. A wide scatter of values is evident (caused by variations in

plankton population, meteorologic conditions, etc.) including some negative values during the hours of 1000–1600. These were associated with dense cloud cover and rain during the interval between pH determinations. The data show a maximal rate of CO₂ removal during the 0700–1000 interval. The mean value for that interval is about 10 μ moles of CO₂ removed per liter of water per hour. The photosynthetic rates were lower during the 1000–1300 and 1300–1600 intervals, yielding a mean of about 6, if the negative values are excluded. During the 1600–1900 interval negative values were observed more often than positive values, and the mean rate computed from the data is about –1, indicating that the respiration rate in the aquatic community during these hours usually exceeded the photosynthesis of the autotrophic component, although the mean light supplies during this time interval (submarine photometer data, Weston photonic cell) were about one-third the mean intensity during the 0700–1000 interval. On the basis of photosynthesis vs. light intensity curves (Verduin 1956a) a rate about one-half as high as the 0700–1000 rate would be expected, rather than the negative average rate appearing in Figure 1. During the hours of darkness negative values were observed, indicating a mean respiration rate of about 6 μ moles of CO₂ evolved per liter per hour.

The low rates of photosynthesis observed during the late afternoon are similar to the decline in activity observed by Doty and Oguri in samples collected during this time of day. Their methods were quite different,

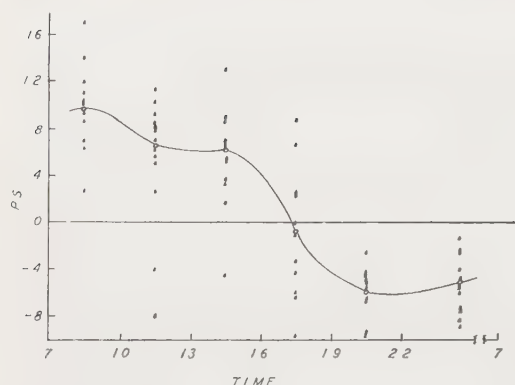


FIG. 1. Hourly carbon dioxide removal (PS, $\mu\text{moles/L}$) against time of day. The values below the line in the 10-13 and 13-16 intervals were associated with dense cloud cover and were excluded in computing the average values (circles).

employing radioactive carbon and exposing collections to uniform light. They consider their results to represent net photosynthesis, but this does not mean that the respiration by consumer components of the community is subtracted from the photosynthetic total as is the case under the completely natural conditions obtained in Lake Erie. The data of Jackson and McFadden (1954) under natural conditions in Pymatuning Reservoir, and the data of Odum (1957, his figures 23 and 24) also indicate a pronounced decline in photosynthetic rate during the afternoon. This fact is not immediately apparent from Odum's figures, because he graphs O_2 concentration against time of day. The curves show a downward trend soon after midday, indicating that O_2 consumption exceeded O_2 production throughout most of the afternoon, although light intensities were favorable for photosynthesis. It seems likely that this is a common phenomenon in natural communities. I reported in a previous paper (Verduin 1956a) that phytoplankton enclosed in bottles showed a pronounced decline in photosynthetic rate after about eight hours of exposure to light. Students of algal photosynthesis in laboratory culture have long been aware of a decline in photosynthetic rate with prolonged illumination and have noted that the decline is proportional to intensity of light (Rabinowitch 1945: 534). The various factors which may contribute to this decline (accumulation of

products of photosynthesis, photautoxidation, narcosis, variations in respiration rate) are discussed by Rabinowitch in appropriate chapters (see also Vol. II, Part 1, Chapters 26 and 28). But the occurrence of such a decline during daylight hours under natural conditions has apparently not been studied very intensively.

Yentsch and Ryther (1957) reported a two-fold increase in chlorophyll concentration during the hours 1600-0800 in carboys suspended at the surface in Woods Hole Harbor. An 0800 collection also showed twice as much C^{14} up-take as the 2400 collection. These data suggest that chlorophyll destruction in superoptimal light may contribute to the reduction in rates as the day progresses, and that recovery of chlorophyll concentration during night hours may contribute to the high photosynthetic capacity during early daylight hours. Doty and Oguri, however, (footnote p. 39) state that "studies in the Pacific have revealed no relationship between chlorophyll content of the water and carbon fixation." Moreover, Figure 2 of Doty and Oguri shows that samples taken from a depth of 20 meters at 1900 exhibited the same low rates as surface collections. If destruction of chlorophyll in superoptimal light were contributing importantly to the decrease in photosynthesis, the samples collected from a depth of 20 meters should have exhibited a less pronounced inhibition.

Doty and Oguri speculate about the possibility that respiration rates increase so much that the net photosynthetic rate is reduced while total photosynthesis may continue at a high rate. This seems an unlikely explanation, at least in Lake Erie. The decline in rate I observed in samples enclosed in bottles (1956a) was a decline in total, not net photosynthesis; clear and darkened bottles were used. However, an increased respiration rate is evident after several hours exposure to saturating light intensities.

During the Lake Erie photosynthesis studies using samples enclosed in bottles (1956a) I regularly measured respiration rates of the samples which had been exposed to optimal light intensities by transferring

them to dark bottles and measuring CO_2 evolution (i) during the five-hour interval immediately following the photosynthesis tests and (ii) for an additional twelve-hour interval. The average respiration rate (38 samples) during the five-hour interval immediately following the period of illumination was $0.58 \mu\text{moles CO}_2$ evolved per 10 μliters of phytoplankton per hour; the average rate during the additional twelve hour interval was 0.34. An increase in respiration rate following illumination has also been observed by the students of *Chlorella* photosynthesis. Brackett, Olson, and Crickard, 1953, reported a four-fold increase in respiration rate after 18 minutes of illumination. They have been inclined to regard it as a nuisance, rather than an interesting phenomenon, because it makes the respiration correction during periods of illumination unreliable.

Whatever the causes of the variation in photosynthetic rates during daylight hours, it is a phenomenon of importance to the student of photosynthesis under natural conditions. Most estimates of photosynthetic yield per unit area are based on the assumption that photosynthetic rates are proportional to light intensity throughout the day and that a given light intensity at 1700 will support the same photosynthetic activity as at 0900. This assumption has led to refined analyses of light intensity at different hours of the day in the belief that such refinements would improve the estimates of photosynthetic yield (Manning and Juday 1941, Ryther 1956, Talling 1955). It is obvious that the decline in photosynthetic activity as the day progresses invalidates the assumption on which those refined analyses are based. I have argued (Verduin 1956b) that simply assuming an average photosynthetic yield in the euphotic zone equal to 0.65 (the hourly rate under optimal light) and multiplying by the hours of daylight provides a yield estimate in close agreement with the estimates from the detailed calculations of Manning and Juday; and Steemann Nielsen (1951) also was content to give equal weight to each hour of the tropical day. It seems likely that the simple calculations based on these

rough approximations are no less reliable than results of the detailed calculations which involve integration of light intensity with time. It should be recognized that the photosynthetic rates used in any calculation represent a rough approximation of the true rate under natural conditions. It may be that the rates measured during the 3–4 hour interval after a collection has been stored in the dark for several hours (as was the case in the clear and darkened bottle experiments in western Lake Erie) are representative of the high rates during morning hours. If so, then an estimate of daily yield based on the assumption that this high rate persists throughout the day would be about 1.8 times higher than the estimate obtained by assuming that the rate declines to about 60% during the mid-day hours and approaches zero during the last quarter of the daylight period.

Whether the decline in rate is related to the time of day or simply to the duration of exposure to light is also of importance to yield estimates. If the decline is determined by the duration of the exposure to light then a habitat in which a turbulent water column includes an extensive dysphotic zone, so that phytoplankters are not likely to spend more than 4 consecutive hours in the euphotic zone, would be expected to support high photosynthetic rates throughout the daylight hours. A study of phytoplankton collected from highly turbulent epilimnions in which the thickness of the euphotic zone is less than half that of the epilimnion would test this hypothesis.

There is some evidence that the low photosynthetic rates evident in the 1600–1900 interval of Figure 1 are a result of prolonged exposure to light rather than being a periodicity which is closely related to time of day. The wide scatter of values in that interval is noteworthy in this connection. The high values in the group were obtained on days in which rain showers had caused low or negative rates earlier in the day, suggesting that phytoplankters which have been exposed to dim light during the day can carry on high rates of photosynthesis during late afternoon hours.

The data presented here do not provide

confirmation of the phenomenon reported by Doty and Oguri, because the methods of study were different and the work was carried out under completely natural conditions. However, the data do indicate that variations in photosynthetic and respiratory rates with time of day warrant more careful consideration in studies of productivity in aquatic environments, and that yield estimates with an error of less than a factor of two can not be made until such information is obtained.

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The Euphausiid Crustaceans *Thysanopoda aequalis* Hansen and *Thysanopoda subaequalis* Boden, Their Taxonomy and Distribution in the Pacific¹

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ABSTRACT

The original specific criteria given for *Thysanopoda subaequalis* are shown to be unreliable. However, on fresh morphological and distributional evidence it is decided that the species is valid. Its diagnosis is modified and the distribution of the species, in relation with *Thysanopoda aequalis*, is discussed.

*Thysanopoda subaequalis*² was established by Boden (1954) on specimens from the Straits of Mozambique. Its close relationship to *T. aequalis* was noted and it was pointed out that the frontal plate and first antennal peduncle of these species had points in common. The main criterion given at that time for separating *T. subaequalis* from *T. aequalis* was the presence of a spine-shaped process on the copulatory organ of the adult male of the former. *T. aequalis* was described as lacking this process (Hansen 1905).

Boden, Johnson, and Brinton (1955) indicated that the first antennal peduncle and spine-shaped process are unreliable as specific criteria and cannot be used to separate *T. subaequalis* from *T. aequalis*.

A critical examination of the copulatory organs has convinced us that the spine-shaped process is normal in both species. In those specimens where it is apparently lacking, there is a detectable scar indicating the insertion position of this process on the innermost margin of the inner lobe. We interpret this as evidence that the process has broken off. This mark is discernible in Hansen's (1910) figure of the copulatory organ of *T. aequalis*.

On the other hand, the frontal plate (Fig. 1) appears to be a more reliable specific

character than was first suspected. This is true in both sexes. In neither species does the frontal plate reach beyond the eyes. In *T. subaequalis* (Fig. 1b, c) it appears fleshy and its anterior margin is thickened; there is no rostral process. The frontal plate of *T. aequalis* (Fig. 1a) lacks this fleshy appearance and, in lateral view, the anterior margin tends to taper; in some specimens the rudiments of a rostral process can be discerned.

The endopodite of the third thoracic leg of the adult male of *T. subaequalis* is its most striking specific character. The propodal segment is greatly reduced, and the dactylus is modified as a long, naked spine (Fig. 2a, b). This modification was not mentioned when *T. aequalis* was described (Hansen 1905). It was described as a sexually dimorphic character of this species by Zimmer (1914) and Tattersall (1924), who did not realize that they were dealing with a separate species.

T. aequalis and *T. subaequalis* are similar, if not identical, in respect to the morphological characters which have heretofore been considered of primary importance in euphausiid taxonomy (e.g. eyes, male copulatory organ, antennal peduncle), indicating a possible subspecific relationship between them. The genetic basis for the diagnostic character described above could conceivably result in intergrades between *T. aequalis* and *T. subaequalis* being indistinguishable as such—an animal might either have the spine or not. However, while there is some overlap in the geographical ranges of the

¹ Contribution from the Scripps Institution of Oceanography, New Series, No. 949.

² British Museum (Natural History) type specimen registered no. 1951.IV.2.1. Additional specimens have been deposited at the U. S. National Museum and at the Scripps Institution of Oceanography (Division of Marine Biology).



FIG. 1. Frontal plates in lateral aspect: a) *T. aequalis*; b) and c) *T. subaequalis*.

two forms (Fig. 3) we have no evidence regarding their possible reproductive isolation or compatibility, and we consider that they should be retained as distinct species.

The lateral aspect of the frontal plate has proved to be an almost invariably reliable means of separating the two species: only a few of the individuals examined have the third thoracic leg modified and the frontal plate tapered (Fig. 1b).

It has not been possible to distinguish be-

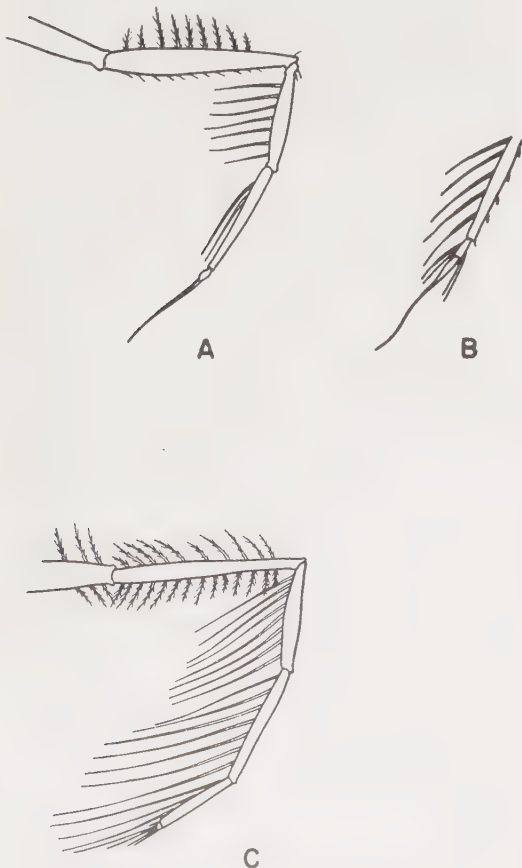


FIG. 2. Endopodite of third thoracic leg: a) *T. subaequalis* (adult); b) *T. subaequalis* (12.5 mm young specimen); c) *T. aequalis*.

tween larval specimens of the two species, but on the basis of the distribution of the adults they may often be assigned with reasonable certainty to either *T. aequalis* or *T. subaequalis*.

Immature individuals cannot be separated reliably. In *T. subaequalis* the dactylus of the third thoracic leg of the male is not modified until the onset of maturity, at a length of about 12.5 mm. Instars of this length carry the modified dactylus in addition to a number of normal setae on the reduced propodus (Fig. 2b). Specimens longer than 13 mm, which stage is probably attained with the succeeding ecdysis, bear only the naked terminal spine.

MATERIALS AND METHODS

The collections utilized in this study were made during a series of cruises carried out by the Scripps Institution of Oceanography from 1950 to 1956 as follows: "Mid-Pacific" Expedition (1950), east and southeast of the Hawaiian Islands; "Northern Holiday" Expedition (1951), Gulf of Alaska to 27°N, northeast of the Hawaiian Islands; "Shellback" Expedition (1952), eastern equatorial Pacific; "Capricorn" Expedition (1952-53), Equatorial Pacific, 170°E to 120°W; "Transpacific" Expedition (1953), northern Pacific, including Bering Sea, waters east and northeast of Japan, and the mid-central Pacific; "Troll" operation (1955), western equatorial Pacific; "Norpac" Expedition (1955), east of 150°W, between 49°N and 20°N; "Chinook" Expedition (1956), Aleutian to Hawaiian Islands; "Equapac" Expedition (1956), equatorial Pacific near 160°E, and 160-175°W. Material from a 1951 cruise to the mid-equatorial Pacific was kindly made available by the Pacific Oceanic Fishery Investigations of the U. S. Fish and Wildlife Service.

Net-tows were oblique, usually from depths of 140 or 300 meters. A one-meter plankton net of 0.5-0.6 mm mesh with an Atlas flow meter in the mouth (King and Demond 1953) was used. An opening and closing release mechanism (Leavitt 1935) was used for collections on which the vertical distribution pattern is based. A detailed discussion of collection methods and data

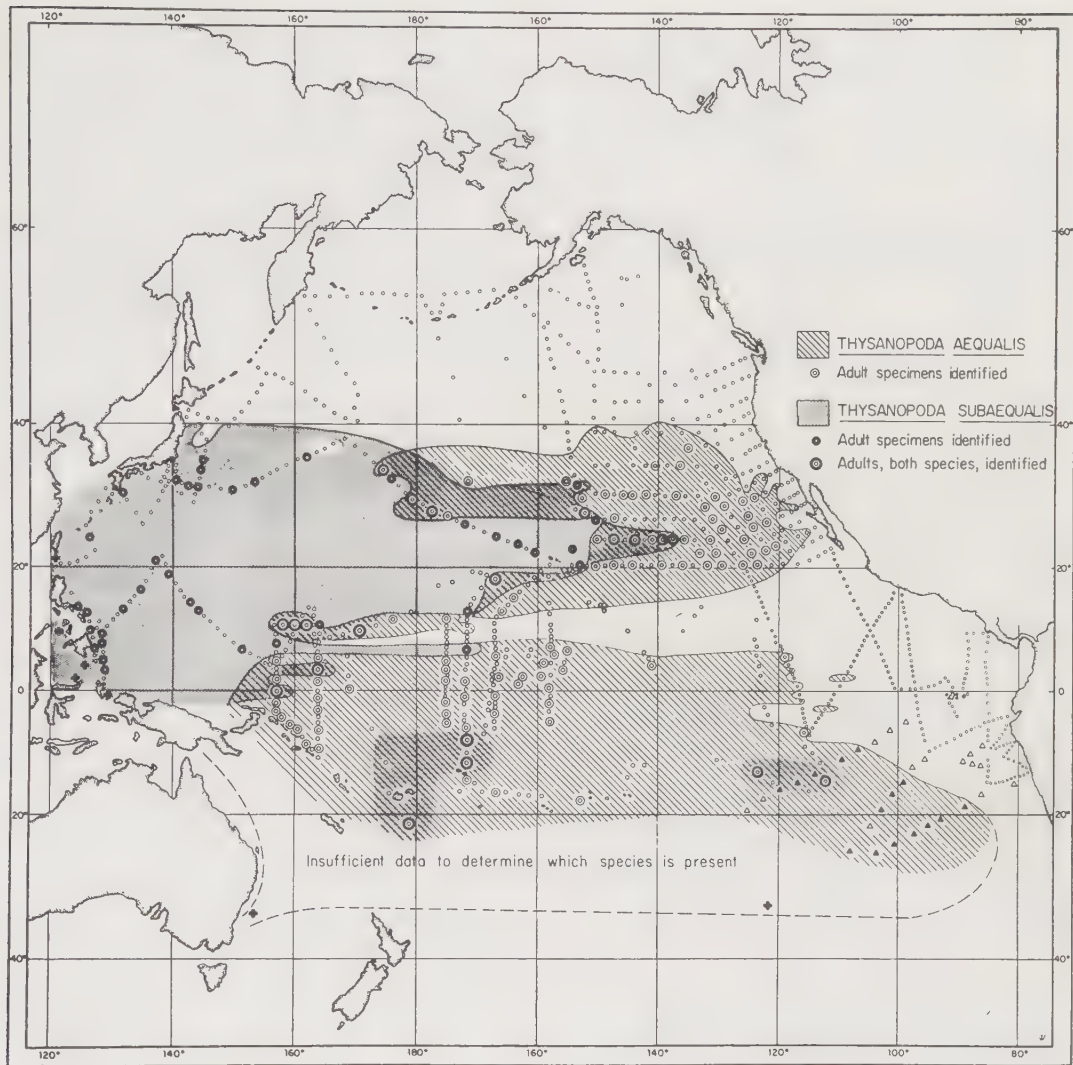


FIG. 3. Horizontal distribution of *T. aequalis* and *T. subaequalis* in the Pacific based mainly upon Scripps Institution collections (see text). Small circles outside shaded or cross-hatched areas are stations at which no specimens of either species were taken. Similar circles within these areas represent stations at which immature or larval forms occurred. Triangles are "Albatross" stations (Hansen 1912). Solid triangles are positive *T. aequalis* records, while open triangles are negative. Crosses are records for *T. aequalis* from Hansen (1910, 1915, 1916) and Sheard (1953).

analysis will appear in a forthcoming paper on the distribution of Pacific euphausiids (Brinton, in preparation).

HORIZONTAL DISTRIBUTION

The composite range of *T. aequalis* and *T. subaequalis* (Fig. 3) extends from 40°N to at least 33°S in the eastern South Pacific (Hansen 1915) and to 34°S in the western South Pacific (Sheard 1955). Both species

are missing from the eastern equatorial basin and from a tongue-like westward extension of equatorial waters reaching to at least 175°W, with an east-west axis at 9°–10°N. These species were lacking at a single station (8°N) on a north-south line of stations, at 164°E, occupied during "Equapac" Cruise, 1956. On the basis of this negative record, the area from which these species are apparently excluded is tentatively extended to

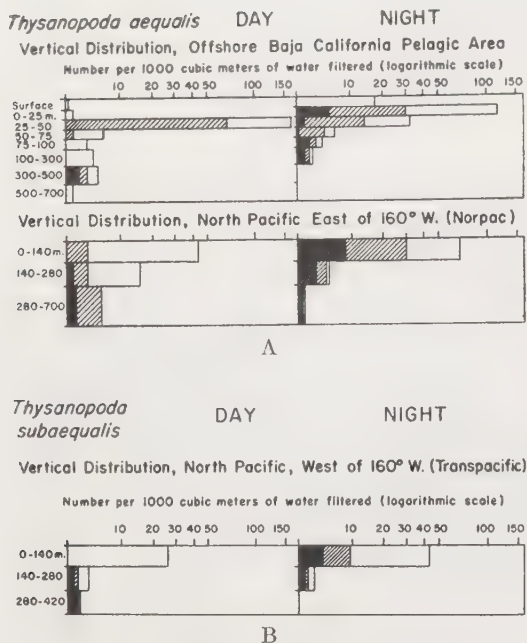


FIG. 4. a) Vertical distribution of *T. aequalis* in the Baja California Pelagic Area (a local area) in April, 1953, and in the larger "Norpac" area (see text) in 1955. b) Vertical distribution of *T. subaequalis* based on collections of the "Transpacific" Expedition (see text). In both a) and b) adults are indicated by the solid black bars, immature specimens by the cross-hatched bars, and furcilia larvae by the open bars. The number of specimens at each depth is the average collected at stations within the ranges of the two species on the above expeditions.

164°E (Fig. 3). The distribution of *T. subaequalis* is based upon identification of 300 adults in 58 collections; that of *T. aequalis* is based upon identification of 550 adults in 110 collections.

The 11° isotherm at 200 meters (Chart IV, Sverdrup, Johnson, and Fleming 1946) which follows the pattern of current flow in the central waters of the North Pacific, closely parallels the margin of the combined distribution of these species, and is associated with the tongue-like area of exclusion in the western equatorial Pacific. The temperature at 200 meters in the eastern equatorial basin south of 8°-10°N, including the Peru Current, is thus high enough to be within the postulated tolerance of *T. aequalis*. This species does, in fact, penetrate eastward to 110°W in the latitude of

the equatorial countercurrent. However, the predominant direction of the currents is from east to west in the western equatorial region. The North Equatorial Current arises, in part, in the oxygen-poor waters off Mexico and Central America, while the South Equatorial Current derives some water from the colder part of the southern hemisphere via the Peru Current. The regions of origin of both of these currents appear to be unsuitable for these species, and to be outside their apparent geographic range.

T. aequalis is present in the cooler parts of the composite range in the North Pacific where the temperature of 200 meters approximates 11° to 16°C; *T. subaequalis* is predominant in a warmer western zone where the temperature at that depth is higher than 16°. *T. aequalis* occurs throughout the composite range of the two species in the South Pacific, whereas *T. subaequalis* appears to be limited to the warmer portion, approximately confined by the 21° isotherm at 200 meters.

VERTICAL DISTRIBUTION

The vertical ranges of these two species in the North Pacific appear to be the same (Figs. 4a and b). Furcilia larvae, which show no tendency to perform diurnal vertical migrations, occur above 280 meters. Adults are present below 140 meters during the day and move into the 0-280 meter layer at night. Most immature individuals are present above 140 meters at night.

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Phytoplankton Studies in Lower Narragansett Bay¹

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ABSTRACT

A total of 82 surface samples were collected at three stations in lower Narragansett Bay from June 1954 through February 1955. Measurements of temperature, salinity, transparency, phosphate, iron, and oxygen were made, and 75 production and nutrient metabolism experiments were conducted.

Maximum phytoplankton populations were encountered in September and January, the mean standing crop being considerably in excess of that recorded in adjacent areas. Two hurricanes evoked a vigorous response in the phytoplankton. *Skeletonema costatum* accounted for 81.2 per cent of the total population. Subsidence of the late winter flowering coincided with minimal phosphate concentrations. The development of the September maximum may reflect a decreased grazing rate. The role of stability and the degree of enclosure in the development of phytoplankton populations in protected areas are discussed.

An "atypical" phosphate cycle was encountered in which a summer maximum and a winter minimum occurred. It is postulated that the periods of phytoplankton activity with their accompanying rates of assimilation and regeneration govern this. Three fractions of iron were characterized by marked variations in concentrations.

A mean phosphate assimilation rate of $0.087 \mu\text{g-at./L/day}$ was obtained; regeneration rates were consistently negative. Iron assimilation had to be expressed as trends. On the average, diatoms increased by 53 per cent per day in the light bottle but decreased by 1.2 per cent per day in the dark one. The effect of this on measurements of respiration and gross production were discussed. Average rates of gross production and respiration were 0.43 and $0.32 \text{ ml O}_2/\text{L/day}$, respectively. The annual surface production was calculated to be 84 g C/m^3 whereas it was 64 g C/m^3 during the period of investigation.

INTRODUCTION

Very few investigations have been conducted on the phytoplankton of the North American coasts. Our knowledge is confined almost exclusively to a narrow strand extending from the Gulf of Maine south to Long Island Sound. These studies have revealed that essentially the same factors condition growth here as in European waters. The mingling of boreal and temperate plankton is an outstanding feature of this area.

The investigation reported herein is concerned with one of the largest embayments on the eastern coast: Narragansett Bay. Being an estuary, its composition and dynamics are a little different from that normally encountered in the region as a whole.

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The author is deeply indebted to Dr. David M. Pratt for his continuous guidance and suggestions during all phases of the investigation, to Mr. Donald A. Campbell for his generous assistance, and to Prof. Trygve Braarud and Dr. Robert Conover for reading the manuscript and offering valuable criticism.

TOPOGRAPHY AND HYDROGRAPHY

Narragansett Bay, a 100 square-mile estuary in Rhode Island, is contiguous with Block Island Sound at its mouth and extends inland 35 miles to the mouth of the Providence River. It is subdivided by numerous islands one of which, Conanicut Island, divides the lower reaches into two passages—East and West Passage. The former is the deeper of the two with several pockets over 100 feet and an average depth of 60 feet; the mean depth of West Passage is only 25 feet. Depths are greatest at or near the mouth and steadily diminish inward. Conanicut Island partially blocks the mouth of

the Bay, producing an effective barrier against the intrusion of offshore water masses.

The shallow homogeneous waters of Narragansett Bay possess no constantly well-defined current system. The Bay serves as a drainage basin for many rivers and streams, resulting in a constant slow outward drift of the less saline surface layers through West Passage. Current movements are due primarily to tidal exchanges, the mean maximum flood or ebb velocity being from one-half to one knot over most of the Bay (Haight 1938). In the waters immediately to the south of Narragansett Bay a counter-clockwise drift coming from Martha's Vineyard sweeps in an arc and continues south-westward into Block Island Sound (Powers and Ayers 1951).

METHODS

Sampling procedures

Three stations established in lower Narragansett Bay, which is defined as that area lying between $41^{\circ}36'$ and $41^{\circ}26'$ N (Fig. 1), were sampled approximately weekly from

TABLE 1. *Station characteristics and frequency of sampling*

Station	Mean depth (m)	Prevailing environment	No. of samples collected	No. of productivity experiments
I	2	"Ultra-estuarine"; excessive drainage; frozen over in winter; little exchange with N.B. proper	28	26
II	6	"Estuarine"; drainage minimal; continuous exchange and intermixing of water	29	26
III	6	"Coastal"; transition area between N.B. and B.I.S.	25	23

N.B. = Narragansett Bay; B.I.S. = Block Island Sound.

June 1954 through February 1955. Criteria used in locating the stations were environmental conditions characteristic of the area. Accordingly, Station I is "ultra-estuarine," II "estuarine," and III "coastal." The major characteristics of each station and the frequency of sampling are summarized in Table 1.

All samples were collected within two feet of the surface, usually within two hours of each other at Stations I and II, and the following day at Station III, irrespective of the tidal conditions. An enamel bucket of six-liters capacity served as a collecting device, the contents of which were analyzed for population density, salinity, and oxygen, phosphate, and iron concentrations. At the time of collection, surface and bottom temperature readings were made, along with Secchi disc measurements of transparency. Radiation data, as measured by a pyrheliometer, were kindly supplied by the Eppley Experimental Laboratories of Newport, R. I. Mean monthly values for the year 1954 are given in the appendix. Pertinent meteorological data were obtained from the local (Providence) U.S. Weather Bureau's monthly report, "Local Climatological Data."

Measurement of environmental factors

Phosphate concentrations were determined by the Deniges-Atkins method.

Reducible and "total" iron fractions were determined by Cooper's (1935a) 2,2'-dipyridyl method. Reducible iron, hereafter called "soluble" iron, included both

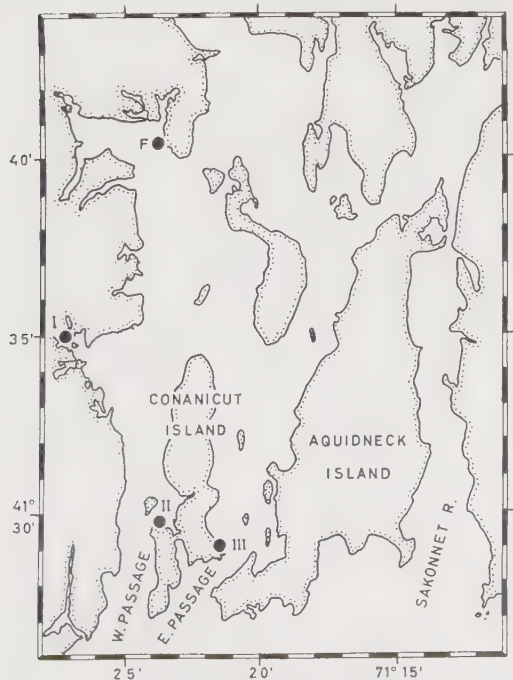


FIG. 1. Station locations in lower Narragansett Bay. F = Ferrara's station in 1952-53.

the ferrous and ferric iron contained in soluble organic and inorganic compounds, along with certain forms of insoluble (particulate) iron. "Total" iron represents that present in "soluble" form plus particulate iron except for that contained in terrigenous material (Cooper 1935a, 1948). "Particulate" iron is defined as the difference between the "total" and "soluble" fractions. This is not entirely in agreement with the accepted definition that the particulate fraction is the difference between the total iron of filtered and unfiltered samples. Unfortunately filtration was not employed, and the term "particulate" iron must be considered with this in mind.

Dissolved oxygen was measured by the Winkler method.

Salinity was determined by silver nitrate titration or hydrometers.

Phytoplankton abundance was estimated by using a Sedgewick-Rafter counting chamber. All counts were made on non-preserved samples within one day after collecting. The number of aliquots counted varied with population density, the results of this method of enumeration being considered representative of all but the rarest forms.

Productivity experiments

At the time of sampling, productivity experiments employing Gran's dark and light bottle method were conducted. Two light (*i.e.* transparent) and two dark (opaque) citrate bottles of 380 ml capacity were filled with unfiltered seawater and suspended at a depth of two feet where they remained for 48 hours (in some instances 24 or 72 hours). Upon collection, one light and one dark bottle were fixed immediately for oxygen determinations. The other two were analyzed for population density and phosphate and iron concentrations employing the methods given above. Since the initial concentration of these factors had been determined previously, the reproductive capacity of the phytoplankton and the rates of change of the phosphorus and iron taking place during the productivity experiments could be calculated.

Reproductive capacity (k), or the co-

efficient of change of population per unit of population per day, was calculated by the formula given by Riley (1952a):

$$k = \frac{\ln F - \ln I}{T}$$

where I and F are the initial and final cell concentrations, respectively, and T is the time in days.

The rates of phosphate assimilation and regeneration were measured by the methods given by Pratt (1950). The assimilation rate, or the rate of utilization of dissolved inorganic phosphate, is equivalent to the change in phosphate concentration in the dark bottle (DB) less the change in the light bottle (LB):

$$\text{Ass. rate} = \Delta\text{PO}_4(\text{DB}) - \Delta\text{PO}_4(\text{LB}).$$

The regeneration rate, or rate at which organic phosphorus is converted into inorganic phosphate, is equal to the change in phosphate concentration in the dark bottle:

$$\text{Reg. rate} = \Delta\text{PO}_4(\text{DB}).$$

Iron data had to be expressed as general trends, rather than in terms of the rates of assimilation and regeneration.

SEASONAL CYCLE OF PHYTOPLANKTON

In discussing the cycle of events in lower Narragansett Bay, two facts must be emphasized: (1) only the surface population was sampled, and (2) two hurricanes of considerable impact ("Carol" on 31 August and "Edna" on 11 September 1954) occurred. These storms, especially "Carol," evoked a drastic response of the population; how much this deviated from the normal at this time of year can be shown only by subsequent investigations.

The populations resident at the three stations were nearly identical qualitatively, undergoing similar seasonal changes and responses. Neglecting quantitative differences for the moment, the mean standing crop of the stations combined shows three well-defined maxima: two in September and the third in January (Fig. 2). (The bimodal peak in September will be treated as a single maximum hereafter.) Through June

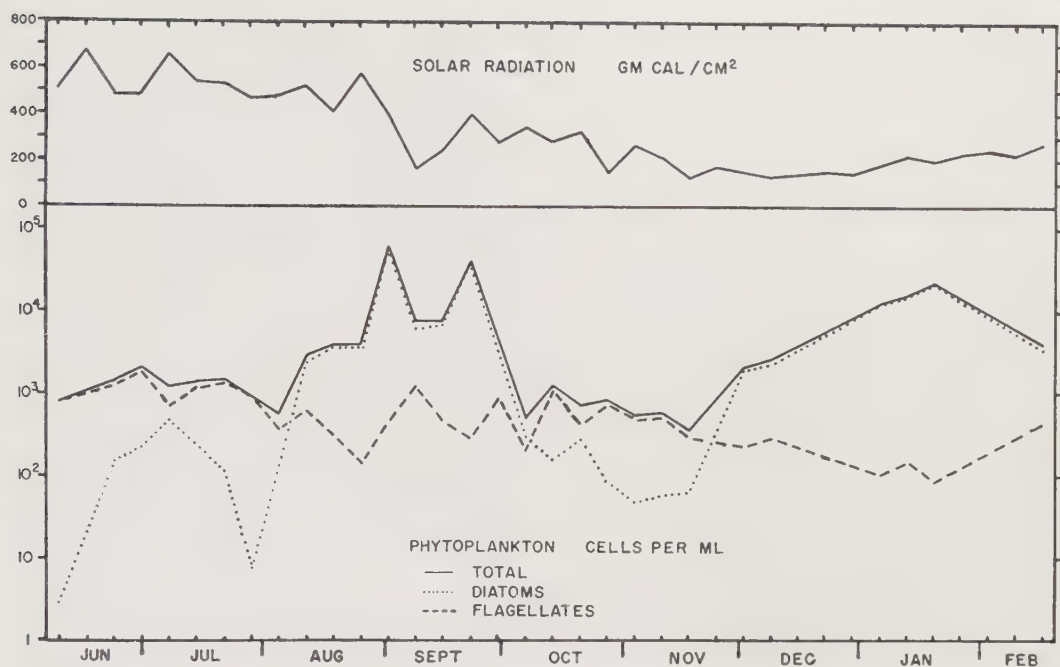


FIG. 2. Seasonal cycle of the phytoplankton population in lower Narragansett Bay (mean of all stations) and solar radiation.

and July the population was at an ebb and showed the first signs of activity at the beginning of August. A population of sizeable magnitude developed through August and then underwent a precipitous increase resulting in a maximum during the first week of September. Thereafter, it subsided during the following two weeks and rose to another maximum during the last week in September; by the second week in October all traces of the flowering had disappeared. The development of a late summer maximum is in agreement with Ferrara's (1953) findings for upper Narragansett Bay. It may occur in the interval between mid-July and October in adjacent waters (Fish 1925, Lillick 1937, Riley 1952a, and Conover 1956).

It seems more than coincidental that the two September maxima occurred immediately following the aforementioned hurricanes. The immediate result of these storms was to increase the phosphate and iron concentrations as well as the turbidity. However, the reduction in transparency appeared not to be a hindrance to active growth since significant utilization of the increased nutrient supply took place. Per-

haps it can be concluded that the effect of the hurricanes was to increase the nutrient concentrations, thereby intensifying and prolonging the late summer flowering.

From the second week in October through mid-November the lowest concentrations of the investigation were encountered. Thereafter a long-sustained flowering took place culminating in a maximum during mid-January. Although it then began to subside, the population was still of considerable magnitude when observations were terminated in late February. A similar winter maximum was reported by Ferrara (1953) in upper Narragansett Bay. Active production during the winter period with the attainment of a winter maximum is a feature common to adjacent waters (Fish 1925, Lillick 1937, Riley 1952a, Conover 1956).

QUANTITATIVE ASPECTS OF THE PHYTOPLANKTON CYCLE

Although the populations at the three stations resembled each other in composition, they were dissimilar quantitatively. The respective seasonal cycles along with

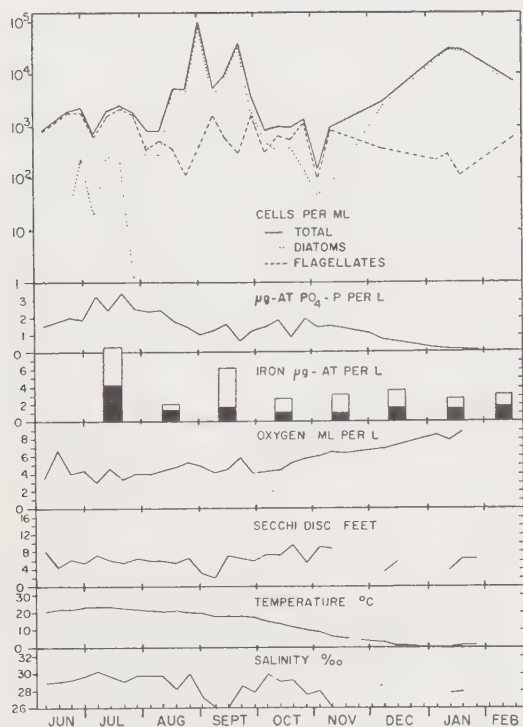


FIG. 3. Seasonal distribution of environmental factors and phytoplankton at Station I. In the bar graph the black portion represents the "insoluble" iron fraction and the clear portion "soluble" iron.

the other factors measured are depicted in Figures 3-5. The mean phytoplankton standing crop for the entire period at Station I amounted to 9.5×10^6 cells/L, almost twice that recorded at Stations II and III where means of 5.5 and 5.2×10^6 , respectively, are representative. The difference between Station I and those in lower Narragansett Bay proper is no doubt attributable to the highly eutrophic conditions associated with excess drainage at the former station.

The data presented above are apt to be misleading since there is no indication of the actual seasonal and quantitative variations exhibited by the local populations. Consequently, four "seasons" have been established to represent particular aspects of the seasonal cycle. The summer season extends from the week of 10 June through 29 July; summer-autumn from 5 August through 7 October; mid-autumn from 14

October through 18 November; and autumn-winter from 25 November through 17 February. The mean seasonal standing crops for the three stations, individually and in combination, are shown in Table 2. Lowest concentrations were recorded in mid-autumn with a mean of 751,000 cells/L. Thereafter, the mean population increased 15-fold to 10×10^6 during the autumn-winter flowering. The mean population during the summer season was approximately 1.4×10^6 cells/L, almost twice that recorded during the mid-autumn lull.

Since Station III could not be sampled until two weeks after the first hurricane, it is necessary to treat the data for the summer-autumn season in two ways: (1) including the results obtained the week after hurricane "Carol," and (2) omitting them. The first method gives a mean total standing crop of approximately 11.5×10^6 cells/L, whereas the second gives almost 8×10^6 . This difference of 40 per cent indicates the hurri-

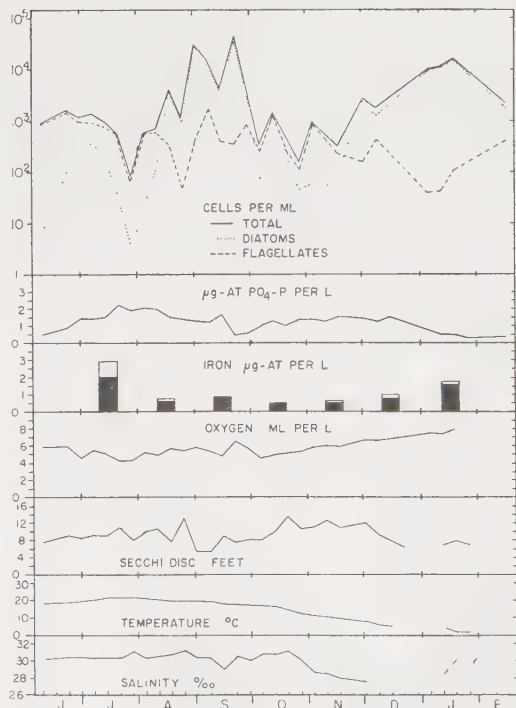


FIG. 4. Seasonal distribution of environmental factors and phytoplankton at Station II. In the bar graph the black portion represents the "insoluble" iron fraction and the clear portion "soluble" iron.

cane's tremendous influence on the population. It becomes even more impressive if the local events prior and subsequent to the hurricane are considered. During the week previous to "Carol" the standing crop at Stations I and II amounted to approximately 5 and 1×10^6 cells/L, respectively. During the week following, totals of 88.5 and 28×10^6 were recorded, or increases of 16- and 27-fold. By the second week a precipitous decrease to 5×10^6 occurred at Station I, while at Station II a sizable population of 13.5×10^6 was still present. It appears logical to conclude that similar responses took place at Station III. Hurricane "Edna" on 11 September appeared to have a lesser effect on the phytoplankton. A retarded response resulted in the development of a maximum after two weeks. Although of substantial proportion it was subordinate to the first one.

The most singular feature of the phytoplankton of lower Narragansett Bay is its extreme abundance compared to other areas. For the same span of year in 1952-1953

TABLE 2. Quantitative distribution of population in cells/ml by season and by station

Seasons	Stations			
	I	II	III	Mean
Summer (6/10-7/29)	1,625	923	1,635	1,359
Summer-Autumn (8/5-10/7)	15,425	10,136	8,278	11,383
Mid-autumn (10/14-11/18)	*7,419	*8,172	*8,278	*7,956
Autumn-Winter (11/25-2/17)	882	642	751	751
	16,777	7,365	7,508	10,180

* Omitting the results of the week following hurricane "Carol."

TABLE 3. Mean standing crop of Narragansett Bay and adjacent areas

Locality	Concentration	
	Cells/m ³	Cells/m ²
Block Island Sound, 1949 (Riley 1952a)	471×10^6	273×10^8
Gulf of Maine, 1933-34 (Bigelow <i>et al.</i> , 1940)	256×10^6	205×10^8
Long Island Sound, 1952-54 (Conover 1956)	2.5×10^9	38×10^9
*lower Narragansett Bay, 1954-55	6.7×10^9	67×10^9
Vineyard Sound, 1935-36 (Lillick 1937)	23×10^6	7.4×10^8

* Mean of nine months; others at least one year.

Ferrara (1953) found a mean of 10×10^6 cells/L in upper Narragansett Bay, as contrasted to an overall mean of 6.7×10^6 for the present investigation. Since his station was located in an environment similar to Station I ("ultra-estuarine"), the comparison should be limited to these two areas. Quantitatively they are very similar: the mean standing crop at Station I being 9.5×10^6 —a difference of 5 per cent.

The mean standing crops of lower Narragansett Bay and adjacent areas are compared in Table 3. Since they are not strictly comparable because of differences in sampling and enumerating techniques, the only value of the table is that it brings into sharp relief the magnitude of the mean standing crop in lower Narragansett Bay relative to the other areas. It tells nothing of the relative production of the areas. It also serves to bring out the apparent relationship between degree of enclosure and mean standing crop. The mean standing crop in the protected waters of Lock Striven and Kiel Bay, 1×10^6 and 627×10^3 cells/L respectively, as contrasted to a mean value of approximately 50×10^3 along the exposed coastline

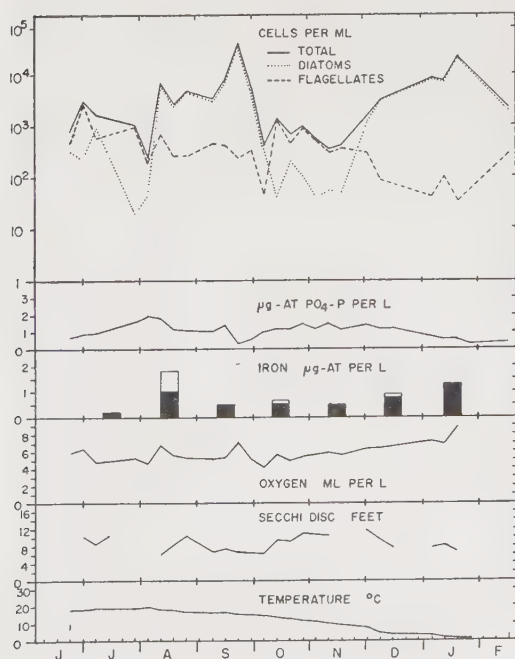


FIG. 5. Seasonal distribution of environmental factors and phytoplankton at Station III. In the bar graph the black portion represents the "insoluble" iron fraction and the clear portion "soluble" iron.

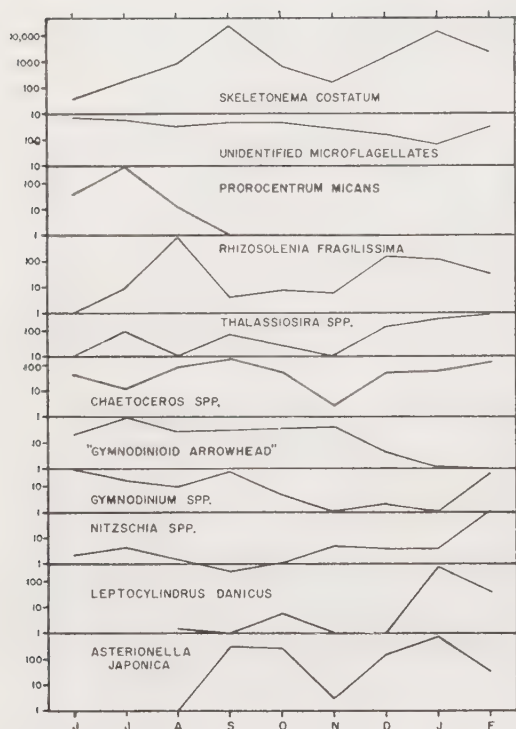


FIG. 6. Seasonal distribution by monthly means, plotted logarithmically, of dominant or persistent members of the total phytoplankton population, expressed as cells/ml.

of California is of interest in this regard (cited by Cupp 1937).

COMPOSITION OF THE PHYTOPLANKTON

Approximately 75 species (see Appendix) were recorded during the investigation, the overwhelming majority being diatoms. The stations were similar in species composition, except for the occasional appearance of tychopelagic and allochthonous forms, always insignificant numerically. The majority of species encountered, however, were subordinate to nine diatoms and four flagellates which accounted for 94 per cent of the total phytoplankton: *Asterionella japonica*, *Chaetoceros curvisetus*, *Leptocylindrus danicus*, *Nitzschia seriata*, *Rhizosolenia fragilissima*, *Skeletonema costatum*, *Thalassiosira gravida*, *T. nordenskiöldii*, *T. rotula*; *Gymnodinium* spp., *Prorocentrum micans*, "Gymnodinioid #1," and micro-flagellates. With the exception of November, one or more of these attained a maximum during each

month (Fig. 6). The pulses of *Skeletonema costatum*, *Thalassiosira rotula*, *Asterionella japonica* and *Chaetoceros* spp. coincided to produce the September maximum. Except for *T. rotula*, these species produced the second maximum in January along with *Leptocylindrus danicus*; *T. nordenskiöldii* and *T. gravida* were important elements as well.

In spite of this succession of maxima, it was almost entirely the variations in numbers of the dominant species *Skeletonema costatum* that determined the seasonal pattern of abundance of the total population. *Skeletonema costatum* was present during all seasons and comprised 81.2 per cent of the total population, in accord with Ferrara's observation that it accounted for 80 per cent of the population in upper Narragansett Bay. It is likewise remarkably abundant in adjacent Block Island Sound where it comprises 83.5 per cent of the total population (Riley 1952a) and is the dominant form in Long Island Sound (Conover 1956). It is an important constituent at Woods Hole (Fish 1925), and occurs the year round in considerable concentrations at Great Pond (Hulburt 1956). Lillick (1937) found *Skeletonema* to be rare in the open coastal waters of Vineyard Sound. It appears, then, that lower Narragansett Bay and its adjacent regions can properly be called a "*Skeletonema* region." That the waters of this region have been remarkably exploited by *Skeletonema* is in line with its apparent preference for semi-enclosed areas. Droop (1955) has shown a vitamin-B₁₂ requirement for this species, and this complex can be expected to occur in appreciable amounts in this type of habitat (Burkholder and Burkholder 1956). These factors coupled with its rapid division rate (Braarud 1937, 1945a) enable it to outstrip its competitors and assert its dominance. As throughout most of its range, it is diamic in lower Narragansett Bay with maxima at a temperature mean of 1°C in January and 18.5°C in September.

Rhizosolenia fragilissima, the second most important diatom, comprised 3.1 per cent of the grand total. Its occurrence was bimodal, the principal peak appearing in August when the temperature was 19°C.

Strangely, Ferrara did not find it in upper Narragansett Bay, and it was rare both in Block Island Sound (Riley 1952a) and at Woods Hole (Fish 1925). On the other hand, it was important in Long Island Sound (Conover 1956).

Asterionella japonica comprised 2.5 per cent of the total population and was bimodal, reaching its first and lesser maximum during September–October when the temperature mean was 16.5°C, and the second during January at a mean of 3°C. Ferrara found it to be rare in upper Narragansett Bay whereas it was numerically important in both Block Island and Long Island Sounds. It appears to be more abundant in lower Narragansett Bay where its cycle supports Conover's contention that it is eurythermal.

Thalassiosira and *Chaetoceros* spp. were of equal importance in lower Narragansett Bay, each constituting approximately 1 per cent of the total population. *Chaetoceros curvisetus* was important during the summer–autumn season. The importance of *Chaetoceros* in the community during the spring is unknown. However, year-round investigations in Block Island and Long Island Sounds (Riley 1952a, Conover 1956) tend to indicate that a *Chaetoceros* vegetation is not the diatom terminal phase in the successional pattern progressing from a *Skeletonema* through a *Thalassiosira* vegetation as it is at Woods Hole (Fish 1925) and certain areas of the Gulf of Maine (Bigelow 1926, Gran and Braarud 1935, Lillick 1940).

Thalassiosira was a persistent genus. *T. rotula* reached a maximum during July at a mean temperature of 17°C and showed a similar peak in September. From November on, both *T. nordenskiöldii* and *T. gravida* increased in numbers and reached a maximum in February, surpassing *Skeletonema* during the latter part of January. *T. nordenskiöldii* was consistently the more important of the two as is the case in adjacent waters. The mean temperature during its maximum was 2.5°C, in close agreement with the 3°C given by Gran and Braarud (1935) as representative for the Gulf of Maine when this species is abundant.

Leptocylindrus danicus accounted for 0.8 per cent of the total population and was

most abundant during January, with a lesser peak during October. Ferrara did not record it in upper Narragansett Bay, and it appears to be more important in both Block Island and Long Island Sounds. As with *Asterionella japonica* its presence in lower Narragansett Bay occurred at a time when Riley (1952a) found it to be absent or rare in Block Island Sound, and conversely.

Nitzschia spp. accounted for 0.1 per cent of the total but never reached the levels of abundance recorded for the adjacent waters, including upper Narragansett Bay. The only important member of this genus was *Nitzschia seriata*, a form which usually occurs in the winter plankton (Lillick 1937).

Dinoflagellates never threatened the superiority of the diatoms. Only *Prorocentrum micans*, which accounted for 0.9 per cent of the total population, was important in spite of its brief occurrence from June through mid-August. It attained a maximum in July when the temperature was 21°C, in close agreement with Barker's (1935) findings that 25°C was the optimal temperature for this species in culture. It appears to be less important in adjacent waters. *Gymnodinium* spp. and a small gymnodinioid (Gymnodinioid #1, designated as "Gymnodinioid arrowhead" in Fig. 6) which eluded identification were persistent but never attained significance.

Unidentified micro-flagellates, however, were quite important accounting for 6.1 per cent of the total population. These forms, which were always present, show a cyclic periodicity in their numbers, of moderate amplitude and with a period of approximately three weeks (Fig. 2). Inspection of Ferrara's data for upper Narragansett Bay reveals a similar periodicity but with a period of two weeks. In both studies this relationship persisted from early summer through November, after which it was not observed. However, the normal sampling routine was interrupted thereafter due to weather conditions. Comparison with adjacent areas is difficult because preservation destroys these forms. The highest concentration recorded for these flagellates was 1.7×10^6 cells per liter, in close agreement with Ferrara's maximum of two million. Riley

(1952a) found "naked flagellates and other small forms" amounting to 10 to 16×10^6 cells per liter during the summer in Long Island Sound. Lillick (1937) recorded a maximum concentration of slightly over 1000 in Vineyard Sound. The considerable abundance and constancy of these micro-flagellates in Narragansett Bay readily indicate their importance in inshore areas, a condition suggested by some authors to apply to the sea in general.

The total diatom and flagellate populations alternated in their domination of the flora. The diatoms were more numerous during the summer-autumn and autumn-winter seasons, whereas the flagellates were dominant during the other two (Fig. 2). In contrast to the diatoms, the flagellates did not show marked maxima and minima but remained relatively constant. Domination of the community by the flagellates was the result of a precipitous decrease in diatom abundance rather than a surge in flagellate numbers as found in the Gulf of Maine (Bigelow 1926).

Except for *Asterionella japonica*, a temperate neritic form, the major diatom species encountered in lower Narragansett Bay (Fig. 6) were members of the boreal neritic plankton element (Gran and Braarud 1935). Although *Peridinium trochoideum* and *Detonula cystifera* were important in upper Narragansett Bay (Ferrara 1953), they were of minor importance during the present investigation.

NUTRIENT CYCLES

Phosphate

The results of the phosphate determinations are given in Table 4. Greatest concentrations were encountered at Station I and approximated those found in Greenwich Harbor, located in upper Narragansett Bay (Ferrara 1953). Station III was similar to

Block Island Sound where Riley (1952a) recorded a mean value of $0.918 \mu\text{g-at./L.}$ The mean concentration for lower Narragansett Bay was $1.26 \mu\text{g-at./L.}$

The classical phosphate cycle in higher latitudes (Sverdrup, Johnson, and Fleming 1942, p. 931) involves a winter maximum and utilization by the phytoplankton during the "spring" resulting in a minimum which usually persists through the summer. In upper Narragansett Bay, Ferrara (1953) discovered an "atypical" phosphate cycle consisting of a summer maximum and a winter minimum.² The same condition was found at all stations in the lower Bay as well. Maximum concentrations occurred in July at Stations I and II and during August at Station III. All stations showed minimal concentrations during January-February (Figs. 3-5). A "normal" phosphate cycle exists in both Block Island Sound (Riley 1952a) and Vineyard Sound (Lillick 1937). Thus the phosphate cycle characteristic of Narragansett Bay is either confined to it exclusively or, more likely, gradually merges with the "normal" cycle in Rhode Island Sound.

The role of accretion in contributing to the observed cycle appears to have been minimal. In spite of excessive drainage into the Mill Creek Basin (Station I) over that of the other areas, especially during July through September, this station did not show a corresponding increase in phosphate concentrations. More likely, the seasonal pattern of assimilation and regeneration controlled the phosphate cycle. Following the attainment of maximum concentrations during late July to early August, the phytoplankton underwent active growth culminating in the September maximum. At all stations approximately 80 per cent of the initial phosphate concentration was consumed, clearly a period in which consumption outweighed regeneration. However, during the ensuing six-week lull regeneration was the dominant process and restored 48.5 per cent

TABLE 4. Results of inorganic phosphate determinations in $\mu\text{g-at./L.}$

Station	Range	Mean
I	0.13-3.20	1.46
II	0.32-2.14	1.20
III	0.33-1.94	1.10

² "Atypical" is used only to distinguish the Narragansett Bay phosphate cycle as contrasted to the one usually observed in stratified waters. The phosphate cycle in Narragansett Bay may eventually be found representative of shallow inshore waters in general.

of the initial phosphate concentration at Station I and approximately 70 per cent at Stations II and III. Thereafter, the continuous sustained winter flowering, which commenced in mid-winter and persisted at the termination of the investigation in late February, made deep inroads on the phosphate supply and created the observed minimum. The phosphate concentrations decreased from 1.86 to 0.13 at Station I, 1.69 to 0.32 at Station II and 1.48 to 0.26 $\mu\text{g-at./L}$ at Station III, or by 82 to 93 per cent. Thus between July and March, except for a six-weeks period from October to mid-November, the rate of assimilation greatly exceeded that of regeneration.

Data from beyond February are lacking. However, the flowering began to subside at this time and undoubtedly terminated during the spring. Accordingly, regeneration would then exceed assimilation and restore the phosphate level to the observed summer maximum. The time of occurrence of this maximum is dependent on when the winter flowering terminates and the ensuing rate of regeneration. The phosphate metabolism experiments revealed regeneration to be a very slow process, in accord with the findings of Cooper (1935b), Riley (1941) and Pratt (1950) among others. Indeed, the mean values for the entire period were negative (Table 6). Positive values were obtained only during August and September at Station I, June and September at Station II, and January at Station III. Thus, a fairly long period may be necessary for the accumulation of regenerated phosphate to maximal concentrations.

That the periods of maximal phytoplankton activity determine, or strongly influence, the seasonal pattern of the phosphate maximum and minimum is not surprising. In general, as the major bloom is displaced farther into the winter or spring, using Narragansett Bay as a reference point, the period of maximum phosphate concentrations is correspondingly displaced. The appearance of a summer or autumn phytoplankton maximum may delay the appearance of the phosphate maximum. The fall overturn may determine when the maximum will be observed in the upper layers.

A phosphate cycle similar to that in Narragansett Bay has been reported from Chesapeake Bay (Newcombe and Long 1939, Newcombe 1940, Newcombe and Brust 1940) and the Isefjord, Denmark (Steeman Nielsen 1951). A direct relationship between phosphate concentrations and turbidity was found in Chesapeake Bay and the hypothesis advanced that heavy rainfall raised the turbidity thus retarding plant growth and allowing phosphate to accumulate. Low turbidities during the winter resulted in increased phytoplankton growth and subsequent diminution of phosphate to minimal concentrations. Newcombe's explanation, however, is not applicable to Narragansett Bay where increased turbidity usually results from dense phytoplankton rather than terrigenous matter. Undoubtedly, the leaching of phosphate from the suspensoids is a factor to be considered in Chesapeake Bay. It is of interest to note that the phytoplankton of Chesapeake Bay shows a cycle similar to that found in lower Narragansett Bay (Morse 1947).

Steeman Nielsen (1951) explained the summer phosphate maximum in Isefjord, Denmark, as a result of regeneration in the bottom muds during this period and subsequent diffusion by convection. This explanation is not inconsonant with the one proposed for Narragansett Bay since its emphasis is on the location of regeneration and not the ultimate source or underlying reason. Since both areas are probably too shallow for the cycle to be completed in the water column as in the Gulf of Maine (Redfield, Smith, and Ketchum 1937), some of the phytoplankton undoubtedly settles to the bottom and decomposes. The excess of interstitial phosphate, available for leaching into the water column, over that adsorbed is a function of many physical, chemical and biological factors (Rochford 1951). The appearance of localized summer maxima in certain Icelandic fjords and elsewhere can be explained as a result of mixing and upwelling (Marshall and Orr 1927, Steeman Nielsen 1935).

Iron

Since the recorded iron concentrations were extremely variable, the data are pre-

TABLE 5. *Results of iron determinations in $\mu\text{g at./L}$*

Station	"Total"		"Soluble"		"Insoluble"	
	Range	Mean	Range	Mean	Range	Mean
I	0.70-12.57	3.57	0.18-10.35	2.14	0.24-7.18	1.69
II	0.0-8.25	1.05	0.0-2.85	0.20	0.0-5.40	0.87
III	0.0-2.55	0.90	0.0-2.15	0.19	0.0-2.80	0.74

sented as monthly averages (Figs. 3-5). This is in line with Cooper's (1948) findings that total iron is randomly distributed and is best studied by using mean values.

The results of the iron determinations are summarized in Table 5. As with phosphate, the greatest mean concentrations of all iron fractions were found at Station I. Stations II and III were similar, the latter exhibiting slightly smaller concentrations. At Station I the mean "soluble" fraction was greater than the "particulate" one. The reverse condition prevailed at Stations II and III. The means of the stations combined were $1.93 \mu\text{g-at./L}$ for "total" iron, 0.88 for the "soluble" fraction, and 0.74 for the "particulate" (insoluble) fraction.

The seasonal cycle at Stations II and III (Figs. 4, 5) suggests a pattern similar to that found by Thompson and Bremner (1935) at Friday Harbor, Puget Sound. There a winter maximum and a spring minimum occurred during which nearly equal concentrations of the soluble and particulate fractions were present. At Stations II and III, however, the particulate fraction accounted for almost all of the iron. Since this fraction measured the iron present in the phytoplankton, the resemblance between lower Narragansett Bay (West and East Passages) and Puget Sound, where filtered samples were analyzed, appears to be only in terms of concentrations.

At Station I (Fig. 3) a completely different situation prevailed. Here the seasonal cycle resembled that of the phosphate cycle typical of Narragansett Bay with a summer maximum and a winter minimum. Unlike Station II and Station III and similar to Puget Sound, the "soluble" and "particulate" fractions were equally abundant.

The "particulate" iron concentrations tended to parallel the phytoplankton stand-

ing crop at all stations except for July at Stations I and II and August at Station III.

NUTRITION AND ORGANIC PRODUCTION

Phosphate metabolism

As with the results of the iron metabolism and organic production only the major features will be considered. A more detailed account will be presented in another paper.

Each station appeared to have its own trend of phosphate assimilation, in spite of the similarities in phytoplankton growth. At Station I the rate increased progressively from June through August with a maximum of $0.48 \mu\text{g-at./L/day}$ occurring on 19 August. It decreased to 0.047 during September, when the phytoplankton reached a maximum, but increased to $0.075 \mu\text{g-at./L/day}$ during October. During November it decreased to approximately the same level as observed in September and dropped again during December. No measurable assimilation was recorded during January and February when the winter flowering was at its peak.

At Station II maximum assimilation was recorded during June ($0.18 \mu\text{g-at./L/day}$), even though the highest individual rate observed was 0.46 during the September flowering. Following June the rate slowly tapered off through August (0.14) and remained at 0.15 during September. It decreased to 0.085 during October and remained at approximately $0.05 \mu\text{g-at./L/day}$ during the winter maximum.

Maximum assimilation was approximately $0.15 \mu\text{g-at./L/day}$ at Station III and coincided with the September flowering. The highest rate recorded was $0.30 \mu\text{g-at./L/day}$ on 16 September. Prior to September the rates increased from 0.09 during July to $0.11 \mu\text{g-at./L/day}$ during August. From October through December the assimilation rate hovered about $0.05 \mu\text{g-at./L/day}$ and then increased to 0.09 during the January phytoplankton maximum.

The rate of assimilation was greater during the September phytoplankton maximum than at any time during the winter flowering. The mean rate at Station I was $0.103 \mu\text{g-at./L/day}$, whereas at Station II and Station III it was 0.075 and 0.082, respec-

tively. The mean of all stations was 0.087 $\mu\text{g-at./L/day}$. Average rates for adjacent waters are similar: 0.114 $\mu\text{g-at./L/day}$ for upper Narragansett Bay (Ferrara 1953) and 0.097 for Long Island Sound (Riley 1941).

It was mentioned previously that "negative" values were usually obtained for regeneration. Maximum recorded rates were 0.16 $\mu\text{g-at./L/day}$ at Station I on 19 August, 0.15 on 16 September at Station II, and 0.075 on 23 September at Station III. The mean regeneration rates were $-0.053 \mu\text{g-at./L/day}$ at Station I, -0.083 at Station II and -0.076 at Station III (Table 6).

Iron metabolism

The nature of the results obtained for the various iron fractions during the productivity experiments precludes consideration of the observed changes in terms of rates of assimilation and regeneration. The results will be expressed as general tendencies rather than as precise rates.

The changes observed in the light bottle were predominantly ones in which both the "particulate" and "soluble" fractions increased. The dominant response in the dark bottle was an increase in the "soluble" fraction accompanied by a decrease in the "insoluble" (particulate) one. This response may be the normal regeneration pathway. When the trend characteristic of a given bottle did not take place, the usual response was that normally found in the other bottle. An infrequent response was one in which there was an increase in the "insoluble" iron with no change in the "soluble" fraction. Regardless of the response in the bottles, the change in the "insoluble" fraction was usually greater than that of the "soluble" one.

Invariably, increases in both fractions corresponded with positive growth coefficients (k) during the growth experiments. Similarly, decreases in both fractions were correlated with negative k values (decrease in the population).

Production

The results of the production measurements are summarized in Table 6. The greatest mean rates of net and gross produc-

TABLE 6. Mean values of productivity and phosphate metabolism experiments (as ml $\text{O}_2/\text{L/day}$ and $\mu\text{g-at. PO}_4\text{-P/L/day}$)

	Stations		
	I	II	III
Net photo-synthesis	0.033	0.353	0.052
Gross photo-synthesis	0.456	0.531	0.311
Respiration	0.412	0.268	0.271
Phosphate assimilation	0.103	0.075	0.082
Phosphate regeneration	-0.053	-0.083	-0.076

tion were recorded at Station II, that station considered most representative of lower Narragansett Bay. Station I showed a lower mean gross production rate and the lowest mean net production rate, in spite of its larger standing crop. The much higher respiration rate at Station I partly accounts for this anomaly. That the respiration value is not completely representative of the phytoplankton but partly attributable to the high detrital content attendant with the run-off is suggestive. The oxidation of organic compounds may also play a part.

In general, gross production rates mirrored fluctuations in the phytoplankton population. They were greatest during periods of maximum phytoplankton activity: August at Station I, September at Station II, and January at Station III. They were lowest during the mid-autumn lull. Greatest net production rates were found during January at Stations I and III and during September at Station II. Similarly, rates were very high during September at the former stations and in January at Station II.

The average rates of gross production and respiration for the stations combined were 0.43 and 0.32 ml $\text{O}_2/\text{L/day}$, respectively. Ferrara, in upper Narragansett Bay, found a higher production rate, 0.61 ml $\text{O}_2/\text{L/day}$, but respiration was similar, 0.32 ml $\text{O}_2/\text{L/day}$. Comparison with adjacent areas is restricted to Long Island Sound where Riley (1941) found the annual mean gross production to be 0.33 ml $\text{O}_2/\text{L/day}$ and 0.17 for respiration. A more recent investiga-

tion (Riley 1956) has revealed a similar gross production value, 0.31, but respiration was only 0.11 ml O₂/L/day. The respiration rate in Narragansett Bay appears to be at least twice that in Long Island Sound. Even if Station I were omitted in the comparison the difference between the two areas would still be quite large, the respiration then being 0.27 ml O₂/L/day in Narragansett Bay.

The mean total phytoplankton production amounted to 0.300 g C/m³/day at Station II, 0.257 at Station I, and 0.162 at Station III. Using the mean gross production rate found for lower Narragansett Bay (0.43 ml O₂/L/day) and assuming it to be representative for the entire year, the production at the surface amounts to 84 g C/m³. A value of 64 g C/m³ is obtained for the period of investigation (June–February). This latter figure is the same as that found for Long Island Sound (Riley 1941), but there it represents the annual surface production. It appears, then, that the surface production in lower Narragansett Bay is greater than that found in Long Island Sound. However, the difference is not so great as would be expected from a comparison of standing crops.

REPRODUCTIVE CAPACITY OF THE PHYTOPLANKTON

The mean growth coefficients (*k*) exhibited by the population during the productivity experiments are given in Table 7. The diatoms and flagellates have been treated separately due to differences in response. The observed growth coefficients indicate only the percentage increase or decrease of the population per day. The maximum *k* value recorded for the diatoms was 1.52, representing an increase from 1700 to 3600

cells/ml. In another instance, the diatom population increased in two days from an initial concentration of 87,000 to 125,000 cells/ml, but the *k* value representing this change was only 0.36.

An average increase in diatom population of 53 per cent per day occurred in the light bottle, whereas the flagellates decreased by 9.5 per cent per day. In the dark bottle both populations usually decreased, the mean being 1.2 per cent per day for the diatoms and 26 per cent per day for the flagellates. These data suggest that it is not valid to assume that similar populations will be maintained in the dark and light bottles during productivity experiments. A diatom increase of 53 per cent per day in the light bottle coupled with a daily decrease of 1.2 per cent in the dark bottle probably will cause a significant difference in the average respiration rates of the two bottles. Since the respiration of the light bottle population must be greater than that in the dark, values obtained from the dark bottle and applied to the light one will be erroneously low. The error thus introduced will give a calculated rate of gross production which is too low. This would partly explain the discrepancy of low production in spite of an enormous mean standing crop in lower Narragansett Bay. A re-examination of the production data from lower Narragansett Bay corrected for the different respiration rates will be treated in another paper.

It is uncertain that these observations are applicable to other areas. The results can not be ascribed entirely to a "bottle effect." The magnitude of the standing crop in lower Narragansett Bay indicates very favorable growth conditions and a correspondingly "active" state of the phytoplankton. The results (light bottle) may be a function of the density and "physiological state" characteristic of the Narragansett Bay phytoplankton. Such attributes would be expected to differ regionally. Conover (1956) apparently found no marked differences in population in her light and dark bottle experiments conducted in Long Island Sound.

In general, the experimental diatom *k* values were considerably higher than those calculated for the natural populations.

TABLE 7. *Reproductive capacity (k) of the phytoplankton*

Station	Diatoms		Flagellates	
	Light bottle	Dark bottle	Light bottle	Dark bottle
I	0.58	-0.044	-0.11	-0.31
II	0.56	0.021	-0.072	-0.31
III	0.45	-0.014	-0.11	-0.17
Mean	0.53	-0.012	-0.095	-0.26

Gaarder and Gran (1927) state that flagellates do not thrive as well as diatoms when confined in flasks and therefore their responses are not representative. Yet in spite of the mean negative k values recorded in both bottles for the flagellates, their responses in the light bottle tended to parallel those in the natural environment.

DISCUSSION

An adequate appraisal of the factors governing phytoplankton growth in lower Narragansett Bay must await further investigation. The following discussion is limited by lack of data and should be considered as provisional.

The waters of lower Narragansett Bay are unstable from September to January inclusive, especially during October through December when the $d\sigma_t$ between the surface and bottom waters is only 0.02. Significant stratification occurs only during April and May when a $d\sigma_t$ of approximately 1.00 is found (Campbell 1953, Hicks and Campbell 1953, Frolander 1955). An over-all shallowness, coupled with significant diurnal turbulence due to tidal exchanges, prevents the development of marked stability in Narragansett Bay (Hicks and Campbell 1953). A thermocline develops at 10 m in the immediate approaches to the Bay during the summer, when none is found inside.

It appears, then, that the winter phytoplankton maximum is coincident with a period of marked turbulence. This suggests that stability is not a prerequisite for the development of the winter maximum in lower Narragansett Bay. The role of stability is one of containment of the phytoplankton enabling the development of a maximum to occur. Instability of the water column results in vertical or horizontal displacement of the crop and prevents the accumulation within the euphotic zone of sufficient numbers capable of producing a maximum. The physical features of Narragansett Bay obviate, or at least restrict, the need for stability. Its over-all shallowness together with a weak surface current satisfy the requirements for a confined population. Exchange with offshore or adjacent waters appears to be minimal

(Frolander 1955), and thus no serious dilution or horizontal transport of the population at subsurface depths can take place. The physical features of Narragansett Bay suggest it is intermediate between theoretical Cases 3 and 4 of Braarud's classification of water-mass types and stability patterns (Braarud, Gaarder, and Grøntved 1953).

The continuous turbulent action taking place during the winter in lower Narragansett Bay, resulting in the constant vertical transport of the phytoplankton out of the productive zone, is probably not deleterious to the population as a whole. The relative shallowness of the water column imposes a limit to dislocation and, since vertical displacement acts in both directions, some of the phytoplankton will be returned to the euphotic zone fairly soon. Since the capacity to assimilate and reproduce is still possessed by the majority of the phytoplankton upon return, they once again become active participants in the community. This repeated transference of the phytoplankton into and out of the productive zone enables the anabolic participation of only a segment of the total population at any given time. The direct result of this cycle is the extended period of continual augmentation, as evidenced by the prolonged period of premaximal activity before the observed maximum. The magnitude and time of appearance of the maximum is controlled primarily by nutrient supply and extent of grazing. If the phytoplankton were always confined to the productive zone, the available nutrient supply would be consumed more quickly and thus restrict the duration of active growth. Of course, under these circumstances, the maximum would occur earlier, relative to the period of active growth. If conditions for containment of the developing population were not supplied by the "natural" features of Narragansett Bay, it is obvious that dissipation of the incipient population would be an important factor. The appearance of peak concentrations would then have to await the development of a fairly stable water mass.

Some of the adjacent waters are more or less protected and this is reflected in their seasonal cycles. In partially enclosed Long

Island Sound considerable pre-maximal activity takes place, and the bloom occurs later than in lower Narragansett Bay (Conover 1956). It might be that some stability is needed for the final spurt to maximum concentrations in this area. The occurrence of significant pre-maximal activity in Long Island Sound is in line with Riley's (1952b) observation that stability is never great there. The more exposed areas, Block Island and Vineyard Sounds, are more dependent on stabilization because effective containment of the developing population is not possible otherwise. Accordingly, there appears to be little pre-maximal activity but rather a sudden efflorescence (Riley 1952a, Lillick 1937).

In spite of the "atypical" phosphate cycle, the phosphate concentrations appear to be sufficient to support an extensive winter flowering in lower Narragansett Bay. It appears that low light intensity does not seriously hamper development during this time since growth was intense during December when the annual minimum of 140.9 g-cal/cm² prevailed (Fig. 2).

Although termination of the winter flowering was not observed, the population began to subside in February. It is to be noted that the phosphate minimum occurred during January–February; in the dark and light bottles phosphate assimilation was very low during that time. Frolander (1955) observed a zooplankton maximum during December–January at his station in the vicinity of Station II.

Unlike some areas, the development of a late summer or autumn phytoplankton maximum in lower Narragansett Bay appears not to be contingent upon destruction of the thermocline and subsequent replenishment of nutrients to the productive layer. In part, the occurrence of a summer phosphate maximum makes this unnecessary. That phosphate can accumulate in the surface layers during the summer, instead of the near the bottom where most of the regeneration probably takes place, is related to the unstable conditions found in the Bay.

Since phytoplankton can thrive at high temperatures if there is a sufficient nutrient supply (Braarud 1945b), the occurrence of

this maximum is determined by other factors. Frolander (1955) found an abundant zooplankton population during July–August. A rich phytoplankton persists during August and attains a maximum in September. It may be that grazing regulates the development of this maximum, its appearance reflecting reduced grazing. An intensive and persistent grazing would tend to retard it. A similar relationship occurs in some Norwegian fjords (Braarud 1944).

Preliminary grazing estimates suggest a huge excess of phytoplankton over that consumed. This excess probably sinks to the bottom. The possibility that lower Narragansett Bay seeds adjacent waters, especially during the winter, should be considered. Riley (1952b) has shown that surface water moves westward into Block Island Sound between nearby Point Judith and Block Island—an avenue readily accessible to the phytoplankton of lower Narragansett Bay.

SUMMARY

A study has been made of the qualitative and quantitative aspects of phytoplankton in lower Narragansett Bay. Three stations were established and sampled at approximately weekly intervals from June 1954 through February 1955. Along with routine measurements of temperature, salinity, radiation, transparency, phosphate, oxygen, and iron, production and nutrient metabolism studies were conducted. The following were observed:

1. Maximum populations were recorded during the winter, and a secondary peak was observed in September. During the latter, vigorous phytoplankton growth followed the occurrence of two hurricanes. The mean standing crop was considerably greater than that found in adjacent regions, and within Narragansett Bay varied with the habitat.

2. The winter flowering had begun to subside when observations were terminated in February. It was suggested that the development of the fall phytoplankton maximum reflected a decreased grazing rate.

3. Of the 75 species found, only nine diatoms and four flagellates each comprised

0.1 per cent or more of the total population. *Skeletonema costatum* was the most important species and accounted for 81.2 per cent of the total. Narragansett Bay and its adjacent areas have been designated a "Skeletonema region." Except for *Asterionella japonica*, the major diatom species were representatives of the boreal neritic plankton element. Unidentified micro-flagellates were very abundant and showed a cyclic periodicity with a period of three weeks.

4. An "atypical" phosphate cycle was observed, with a summer maximum and a winter minimum, and the hypothesis is advanced that the periods of maximum phytoplankton activity and the accompanying rates of assimilation and regeneration govern this. The mean phosphate concentration was higher than that recorded in adjacent waters.

5. The mean rate of phosphate assimilation was similar to that found in upper Narragansett Bay and Long Island Sound. The rate of assimilation was greater during the September maximum than at any time during the winter flowering. Regeneration rates were extremely low throughout the period of investigation as indicated by the frequency of negative values.

6. Iron concentrations were very variable and two vague seasonal patterns were discerned.

7. The iron fractions showed two dominant trends during the metabolism experiments: an increase in both the "soluble" and "insoluble" fractions in the light bottle, and an increase in the "soluble" fraction accompanied by a decrease in the "insoluble" moiety in the dark bottle. Changes in the "insoluble" fraction paralleled changes in the phytoplankton population.

8. The gross production rates were related to the size of the standing crop and were intermediate between those found for Long Island Sound and upper Narragansett Bay. Different growth responses in the dark and light bottles were discussed as a source of error in gross production calculations. Respiration was twice that recorded in Long Island Sound and equal to that found for upper Narragansett Bay.

9. The role of stability and the degree of

enclosure in the development of phytoplankton populations in protected areas were discussed.

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APPENDIX

Radiation as Monthly Means for 1954
(g cal/cm²/day)

Jan.	152.2	July	537.5
Feb.	257.1	Aug.	481.9
Mar.	375.4	Sept.	318.8
Apr.	432.7	Oct.	270.6
May	476.5	Nov.	192.4
June	551.5	Dec.	140.9

List of Species

Diatoms

Centric forms

Biddulphia sp.
Chaetoceros curvisetus Cleve
Chaetoceros gracilis Schütt
Chaetoceros lorenzianus Grunow
Chaetoceros socialis Lauder
Chaetoceros teres Cleve
Chaetoceros spp.
Corethron hystrix Hensen
Coscinodiscus centralis Ehrenberg
Coscinodiscus excentricus Ehrenberg
Delonula cystifera (Cleve) Gran
Leptocylindrus danicus Cleve
Leptocylindrus minimus Gran
Melosira sulcata (Ehrenberg) Kützing
Melosira sp.
Rhizosolenia alata Brightwell
Rhizosolenia delicatula Cleve
Rhizosolenia fragilissima Bergon
Rhizosolenia stolterfothii Peragallo
Skeletonema costatum (Greville) Cleve
Thalassiosira gravis Cleve
Thalassiosira nordenskiöldii Cleve
Thalassiosira rotula Meunier

Pennate forms

Achnanthes sp.
Amphiprora sp.
Asterionella japonica Cleve
Cocconeis sp.
Fragilaria sp.
Grammatophora marina (Lyngbye) Kützing
Gyrosigma sp.
Licmophora abbreviata Agardh
Navicula sp.
Nitzschia closterium (Ehrenberg) W. Smith
Nitzschia delicatissima Cleve
Nitzschia longissima Ralfs
Nitzschia paradoxa (Gmelin) Grunow
Nitzschia reversa W. Smith
Nitzschia seriata Cleve
Pleurosigma sp.
Striatella unipunctata (Lyngbye) Agardh
Surirella sp.
Thalassionella nitzschioides Grunow
Thalassiothrix longissima Cleve & Grunow

Dinoflagellates

Amphidinium sp.
Ceratium fusus (Ehrenberg) Dujardin
Ceratium lineatum (Ehrenberg) Cleve
Ceratium tripos (O. F. Müller) Nitzsch
Cochlodinium sp.
Dinophysis acuminata Claparede & Lachmann
Exuviella marina Cienkowski

Gymnodinium spp.
Gyrodinium spp.
Peridinium triquetrum (Ehrenberg) Lebour
Peridinium trochoideum (Stein) Lemmermann
Peridinium spp.
Polykrikos sp.
Prorocentrum micans Ehrenberg

Other flagellates, etc.

Chilomonas spp.
Cryptomonas spp.
Distephanus speculum (Ehrenberg) Haeckel
Ebria tripartita (Schumann) Lemmermann

Euglena sp.
Pyramimonas sp.
 "Unidentified micro-flagellates"

Ciliates

Codonella sp.
Mesodinium sp.

Tintinnopsis sp.
Tintinnus sp.

The Effect of Circularly Polarized Light on the Photosynthesis and Chlorophyll *a* Synthesis of Certain Marine Algae¹

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ABSTRACT

The net photosynthesis and chlorophyll *a* synthesis of certain marine algae show a gradation in response to various types of polarized light. Right circularly polarized light increases the net photosynthesis and chlorophyll *a* synthesis as compared with light through neutral density filters, whereas the effect is reversed with left circularly polarized light. This suggests that the receptor pigments are anisotropic and exhibit circular dichroism.

There are contradictory views in the literature on the part played by polarized light in certain photochemical reactions and in photosynthesis. Zurzycki (1955) in a recent paper, reviewed the literature, and disclaimed any significant effects of linearly or circularly polarized light on the photosynthesis of *Lemna trisulca* L. leaves. Rabinowitch (1951), however, has pointed out that chloroplasts may exhibit circular dichroism (*i.e.*, differential absorption of right- and left-handed circularly polarized light), particularly in weak light and when the chloroplast is in the profile position. Measurements of circular dichroism are important aids in the study of the optical properties of compounds.

In the following report some experiments will be described concerning the effects of various types of polarized light on carbon-14 uptake and chlorophyll *a* synthesis in the unicellular marine flagellate, *Dunaliella euchlora*.

One and one-half liters of enriched sea water medium were inoculated with a bacteria-free culture of *Dunaliella euchlora* giving an initial cell concentration of 10^5 cells/ml.

The culture was kept in the dark for two days, and then exposed to approximately 1000 foot-candles of non-polarized fluorescent light at 20°C. After 12 hours the culture contained 2×10^5 cells/ml. Exponential growth continued for four days, and the growth stopped after the fifth day.

During the exponential growth aliquots of the culture were suspended in enriched sea water, and the cell density was adjusted to 1×10^5 to 1.5×10^5 cells/ml. The cell suspension was tagged with carbon-14, after the method of Steemann Nielsen (1952), and siphoned into 35-ml glass-stoppered bottles which were placed in finger bowls blackened so that light could enter only through a three-inch square at the top. Neutral-density or polaroid filters were taped to the top of the finger bowls.

The samples were placed at 20°C under 1000 foot-candles of fluorescent light. With filters this intensity was reduced to 300 to 500 foot-candles, which was above the light saturation of the organisms used (Ryther 1956). After varying lengths of exposure, the samples were filtered on millipore filters, the filters dried, and the radioactivity and chlorophyll *a* content (Yentsch 1957) were determined on samples from each experiment. In a series of similar experiments the rate of oxygen production was measured under polaroid and neutral-density filters. Oxygen production was measured by the Winkler method and corrected for respiration by means of a third sample in a darkened bottle.

A bank of daylight fluorescent lamps, used as a light source, showed no polarization when tested with a polaroid analyzer. Light polarization was obtained by Polaroid HN plastic filters, which circularly polarize light throughout the visible spectrum.

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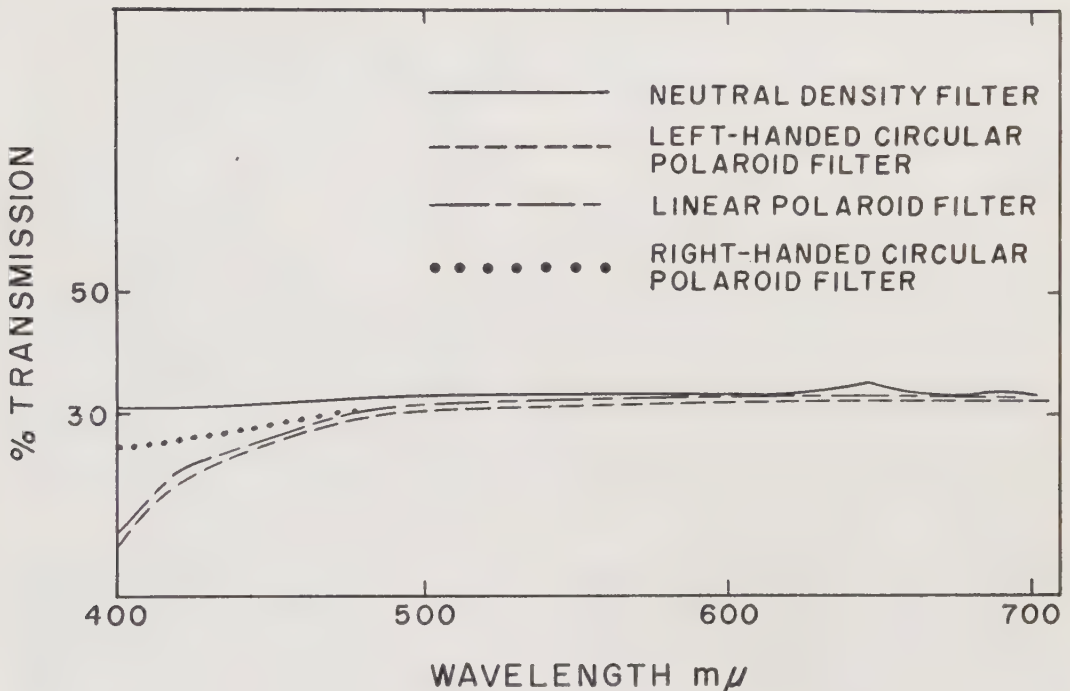


FIG. 1. Transmission curves for polaroid and neutral density filters.

TABLE 1. Per cent transmission of polaroid and neutral-density filter

Filter	% trans- mission
Left-circular polaroid	33.0
Linear polaroid	34.2
Right-circular polaroid	35.8
Neutral-density	37.0

TABLE 2. Mean percentage increase in carbon-14 uptake, chlorophyll a content and oxygen production in *Dunaliella euchlora* under right-circular polaroid filter as compared with neutral-density filter

Light intensity 300-500 foot candles.

Exposure (hours)	Number of experiments	Carbon-14 uptake (cpm)	Chlorophyll a content (mg chl a/L)	Oxygen production (ml/L)
2	3	29	24	
3	2	24	28	
4	3	29	20	5
5	3	23	33	
9	3	35		
10	3	32	17	
15	3	22		
16	3	27	17	14
24	3	26	15	5

TABLE 3. Effect of neutral-density, linear polaroid, and right-circular polaroid filters on the photosynthesis of four unicellular marine organisms

Light intensity 300-500 foot-candles. Exposure 10 hours.

Organisms	Carbon-14 uptake Per cent increase over neutral-density	
	Linear	Right-circular
<i>Dunaliella euchlora</i>	4	25
<i>Porphyridium cruentum</i>	2	29
<i>Skeletonema costatum</i>	0	29
<i>Olisthodiscus</i> sp.	-2	25

TABLE 4. Mean of four experiments showing chlorophyll a content of *Dunaliella euchlora* after ten hours exposure to polarized light

	Filters			
	Neutral-density	Linear polaroid	Right-circular polaroid	Left-circular polaroid
mg chlorophyll a/liter	.22	.24	.30	.17
Percent increase over neutral-density	—	9	36	-23

Three types of polarization were tested: linear, left-handed circular, and right-handed circular polarization. For control measurements, neutral-density filters made from photographic film were mounted on glass plates.

Transmission curves for the polaroid and neutral density filters were plotted from measurements made in a Beckman DU spectrophotometer (Fig. 1). These curves show that the transmission within the visible radiation range is very similar for all filters.

To compare total intensities of the light transmitted by each of the filters, measurements were made with a General Electric Exposure Meter, Type DW-68. The readings indicated that the polaroid filters transmitted less light than the neutral density filters as shown in Table 1.

Table 2 shows the effects of right-handed circularly polarized light on the photosynthesis of *Dunaliella euchlora*. In every case, this type of polarized light significantly increased the carbon-14 uptake and chlorophyll *a* content over that shown by the neutral-density filter.

The differences between values obtained by measuring oxygen production are less than those obtained by measuring carbon-14 uptake. The oxygen values were corrected for respiration and represent total photosynthesis, whereas the carbon-14 uptake is a measure only of photosynthesis above respiration (Ryther 1954). Since respiration was probably rather high compared to photosynthesis at the relatively low light intensities used in these experiments, the percentage differences between net photosynthesis (*i.e.*, total photosynthesis minus respiration) would appear larger than the differences between total photosynthesis.

A series of 10-hour experiments with four different unicellular marine organisms show that in all cases right-handed circularly polarized light increased the photosynthesis (Table 3), whereas there was no significant difference in photosynthesis between the organisms under the neutral-density and the linear polaroid filters.

According to physical theory (Glasstone 1940) there should be a gradation in response to various types of polarization. The ab-

sorption characteristics of linearly polarized light should not differ from those of unpolarized light, but right- and left-handed circularly polarized light should be absorbed to a different extent by the dextro and laevo molecules of an optically active substance.

Table 4 shows the effects of three different polaroid filters on the chlorophyll *a* synthesis of *Dunaliella euchlora*, over a period of ten hours. Again, right-handed circularly polarized light is most effective in chlorophyll *a* synthesis, whereas linearly polarized light is not significantly different from the control. The chlorophyll *a* synthesis with left-handed circularly polarized light, however, is below that of the control. This is in accord with an explanation based on simple circular dichroism of the receptor pigments.

These experiments indicate that chlorophyll *a* production and photosynthesis in certain unicellular marine algae are affected by polarized light, and suggest that the photosynthetic pigments may be anisotropic and exhibit circular dichroism. Waterman (1955) has shown that linearly polarized light penetrates to considerable depths in natural waters. If the same is true of circularly polarized light, it might have ecological significance in photosynthesis under natural conditions.

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The Response of Some Freshwater Fish to Isopropyl Methylphosphonofluoridate (Sarin) in Water

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ABSTRACT

The toxic response and behavior of the fathead minnow (*Pimephales promelas*), the green sunfish (*Lepomis cyanellus*), and the goldfish (*Carassius auratus*) have been determined on exposure to water solutions of isopropyl methylphosphonofluoridate (Sarin). Comparison of the time of response over a wide range of concentrations and at several temperatures for the three species indicates changing rates of reaction to the toxic material. Analysis of the dose-response curves shows that the product of concentration and time of response is not equal to a constant. It is suggested that the point of maximum curvature of the dose-response curve, when plotted on arithmetic paper, be used as a value which would be most consistent for comparing relative toxicities of toxic agents or relative resistance of various species to the same toxic material.

The development of the very potent series of chemical warfare agents popularly known as "nerve gases" has resulted in the need for toxicological information in many species of animals. This paper will describe the response of three species of freshwater fish to water solutions of isopropyl methylphosphonofluoridate (Sarin). This compound has been described by Krop and Kunkel (1954) as a powerful anticholinesterase agent of the alkyl phosphate ester series and has a structure analogous to diisopropyl phosphorofluoridate (DFP).

The response of freshwater fish to this compound has been studied with several purposes in mind. This chemical, which is a watery-looking compound at normal room temperatures, is quite soluble in water and thus permits accurate preparation of desired concentrations in the aqueous medium. The response of fish when exposed to water solutions of Sarin provides a bio-assay for detection of this chemical warfare agent in water, for the study of concentration-time relationships, and for comparative toxicological assessment.

The proposed standard methods suggested

by Doudoroff *et al.* (1951) for the bio-assay of toxic industrial wastes using fish were not deemed particularly suited for our purpose. This method was established primarily for industrial wastes of unknown or mixed chemical composition and was particularly designed for defining that concentration at which 50 % of the fish are able to survive for a specified period of exposure, usually 24 hours or more. A method which would permit the estimation of toxic concentrations by bio-assay required a more precise determination of the 50 % response time at known concentrations of the isopropyl methylphosphonofluoridate. This increase in precision would permit use of fish for determining concentrations of Sarin in water which might be toxic for human consumption.

The isopropyl methylphosphonofluoridate used in these studies was prepared in other laboratories of the Chemical Corps. The compound was synthesized in small batches and was of high purity, 85–90 %, as indicated by chemical assay. Weighed portions of the compound were suitably diluted and then added to 15 liters of water to prepare the concentrations desired for the particular exposure. The water used in these tests was the tap water of the Army Chemical Center. This is a soft water with a total alkalinity of 10–15 ppm. It is treated by coagulation, filtration, and chlorination, and adjusted to a final pH of about 7.5.

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TABLE 1. *Fish species and size ranges used in experiments*

Common name	Scientific name	Weight range	Length range
		g	mm
Fathead minnow	<i>Pimephales promelas</i>	0.75-1.20	25-35
Green sunfish	<i>Lepomis cyanellus</i>	2.0-4.5	45-60
Goldfish	<i>Carassius auratus</i>	1.0-2.5	40-70

The exposure vessels were 12 × 12 inch round glass aquaria calibrated to 15 liters. The test water was dechlorinated by passage through a carbon filter and the pH adjusted to 6.5 by addition of a suitable quantity of 1M KH₂PO₄. The pH adjustment was made to minimize effects of hydrolysis of the Sarin in the longer exposures, up to 24 hours (Epstein 1956). The exposure aquaria were immersed in a large constant temperature tank capable of maintaining the temperature of the vessels at ±0.1°C (Weiss 1955).

The three species of fish (Table 1) employed in this study were obtained from nearby hatcheries and held in 25-gallon stock tanks until used.

The determination of the response of the fish at each toxic concentration was carried out by exposing ten fish simultaneously in the 15-liter aquaria and the time to death (=cessation of all response) noted for each fish. At concentrations in which the time to death of all ten fish was less than 20 minutes the actual time of death of each fish was noted. In the tests which required longer exposures, the number of fish responding at a selected time interval was used rather than the time to death of each fish. In both procedures the accumulated per cent dying was plotted against time of death on logarithmic-probability paper. The 50% response time (T₅₀) was derived from a curve of visual best fit.

RESULTS

A. Behavior and appearance of fish on exposure to Sarin

Exposure of fish to Sarin results in characteristic responses and symptoms. Both the degree and rapidity of response are functions of the toxic concentration but the characteristics of the response were observed

to be the same throughout the range of concentrations studied.

The initial response of the fish on exposure to Sarin is seen in the change from normal movement behavior to rapid darting about with loss of balance. This hyperexcitability is accompanied by sharp tremors which shake the entire fish. The pectoral fins are extended stiffly at right angles from the body instead of showing the usual slow back and forward motion normally used to maintain balance. The gill covers open wide, and opercular movements become more rapid. With death, the mouth is open and gill covers are extended. Hemorrhaging appears around the pectoral girdle and base of the fins. The forward extended, rigid pectoral fins are very characteristic of fish exposed to Sarin, and are particularly noticeable in the sunfish.

In addition to the response behavior of accelerated movement and fin position effect, the sunfish and minnow show a specific response which usually precedes the change in physical activity. When the exposure aquaria are placed over a light colored background and illuminated, the sunfish and minnows become quite pale in appearance or light adapted, due to the concentrating of the skin pigment, melanin, in the melanophores. On exposure to Sarin the fish become uniformly dark. The exposure time necessary to darken is proportional to the concentration of Sarin.

The dispersal of pigment in the melanophores of teleost fish is known to be controlled by dispersing nerve fibers which exert their action through the mediation of acetylcholine. Parker (1940) using eserized fish to prevent the rapid destruction of acetylcholine demonstrated the dispersion of melanin in fish by injection of acetylcholine. The anticholinesterase activity of Sarin to fish (Weiss 1958) may permit the excess accumulation of acetylcholine and cause the light-adapted fish to darken. After death the fish gradually fade to a pale appearance again.

B. The dose-response of minnows, sunfish, and goldfish to Sarin

The response of minnows, sunfish, and goldfish to the toxic action of Sarin over a

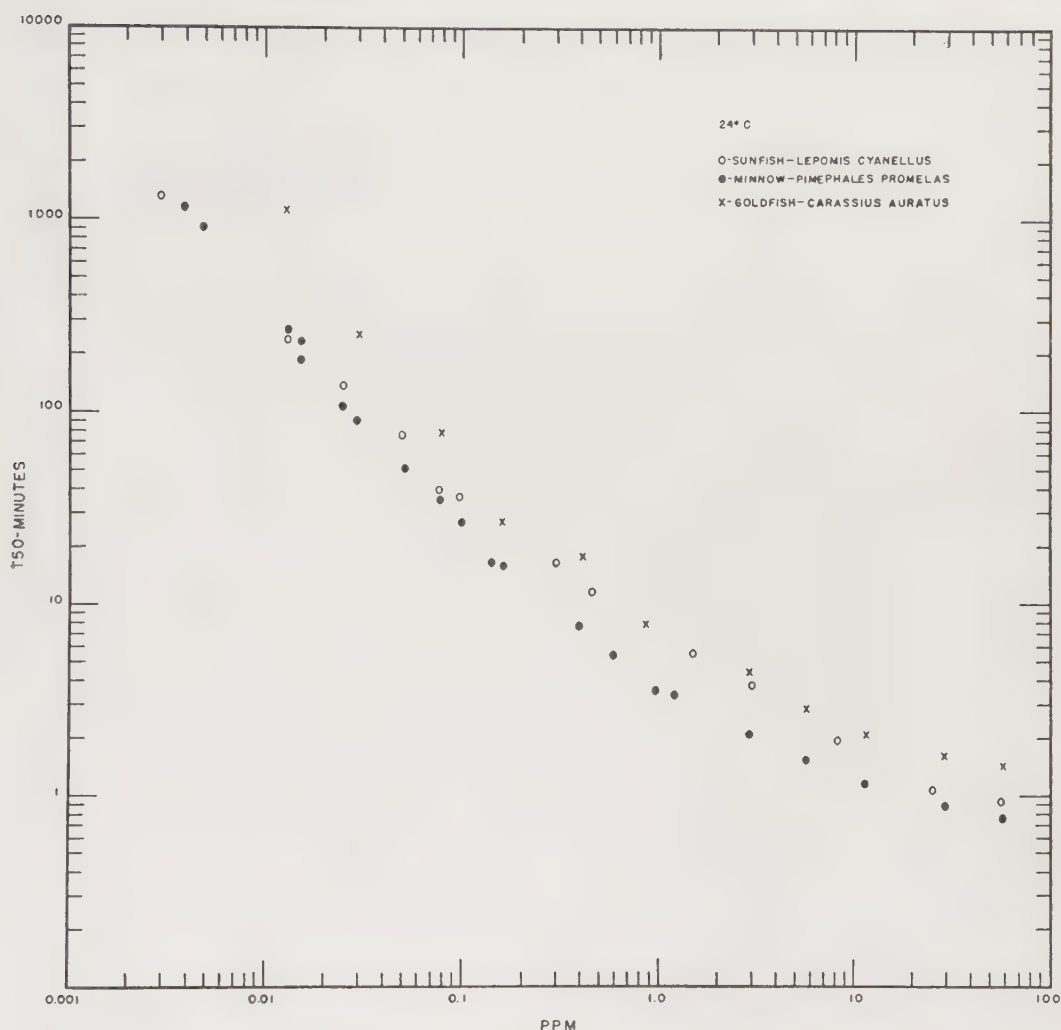


FIG. 1. The dose-response of three species of fish to Sarin at 24°C.

wide range of concentrations at 24°C and 12°C is shown in Figures 1 and 2. A more detailed study of the response of the sunfish at 7.5°, 12°, 17°, and 24°C to Sarin is shown in Figure 3.

The dose-response points presented in Figures 1 and 2 indicate that at both 24°C and 12°C the three species of fish tested consistently maintain the same relative position with respect to each other. That is, at any concentration the response time of the goldfish is longer than that of the sunfish, which in turn is longer than that of the minnow. Of the three species, the sunfish dose-response points tend to have the greater scatter from a smooth line connecting the

points than do the points representing the other fish. At very low concentrations of toxic and consequent long response times the dose-response points of the sunfish and minnow show a tendency to fall along the same curve.

At 12°C although the general shape of the dose-response curve remains the same, the time of response has lengthened. The magnitude of the temperature effect is shown in Table 2. T50's at selected intervals were read from a curve of visual best fit for each species and at each temperature. The change in reaction time was then examined by computing the change in T50 (in minutes) per degree of temperature

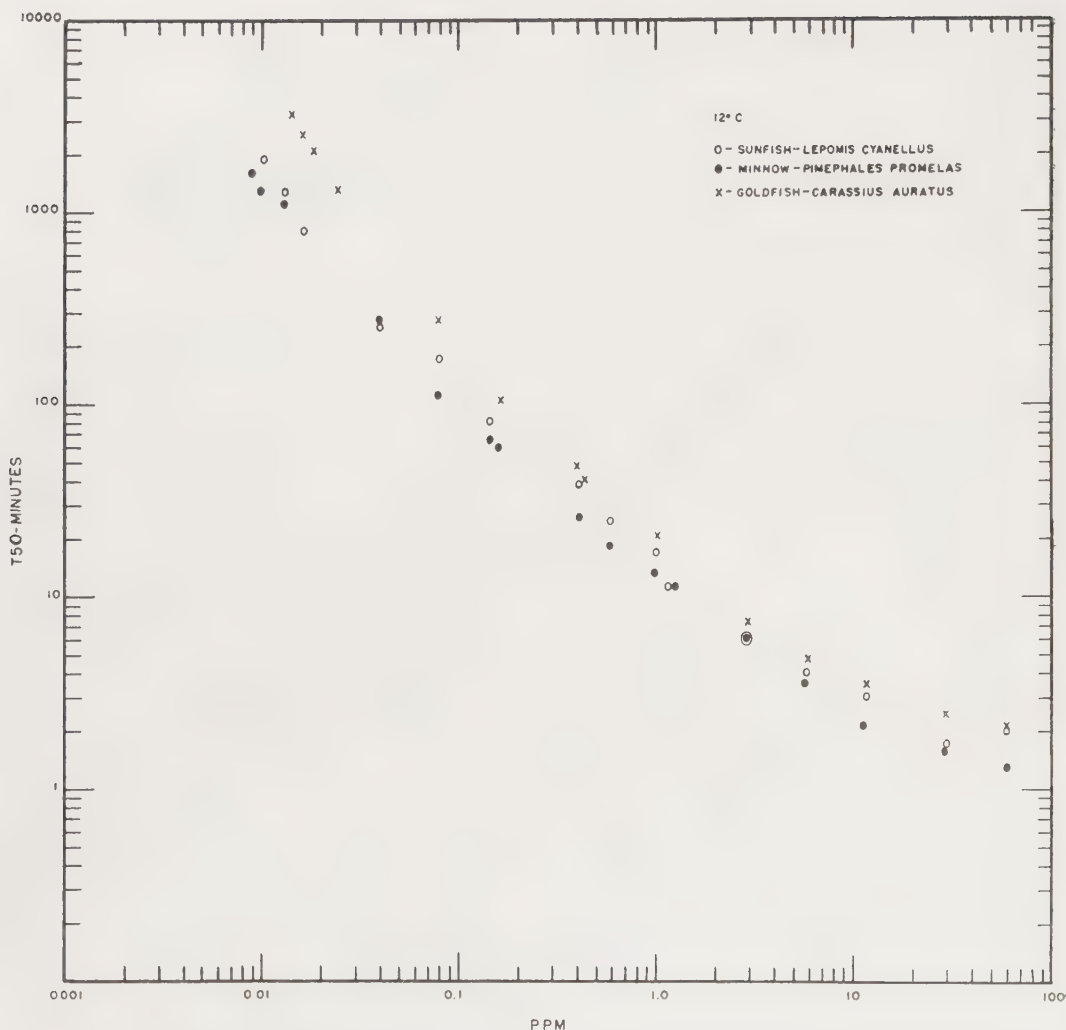


FIG. 2. The dose-response of three species of fish to Sarin at 12°C.

(centigrade) for the 12-degree interval. At all but the lowest concentrations of toxic material the three species show a high degree of consistency in their temperature reaction. The minnow has the smallest change in T50 per degree change in temperature, that for the sunfish is greater, and for the goldfish the largest of the three.

The detailed temperature study with the sunfish, presented in Figure 3, between a more limited range of concentrations, shows the order of magnitude of change of reaction time for the smaller temperature interval. Values of T50 at selected intervals have been determined from the curves of visual

best fit, and the changes in T50 per degree for the three temperature intervals have been calculated and presented in Table 3. These values emphasize the importance of both knowing and controlling the temperature of the assay since small changes of temperature can cause significant changes in T50 relative to concentrations which are considered at or close to the human tolerance levels of water contaminated with Sarin.

The use of small fish as a bio-assay for Sarin appears feasible within the approximate limits set forth by the dose-response curves represented in Figures 1 and 2. The levels of tolerance of humans to Sarin in

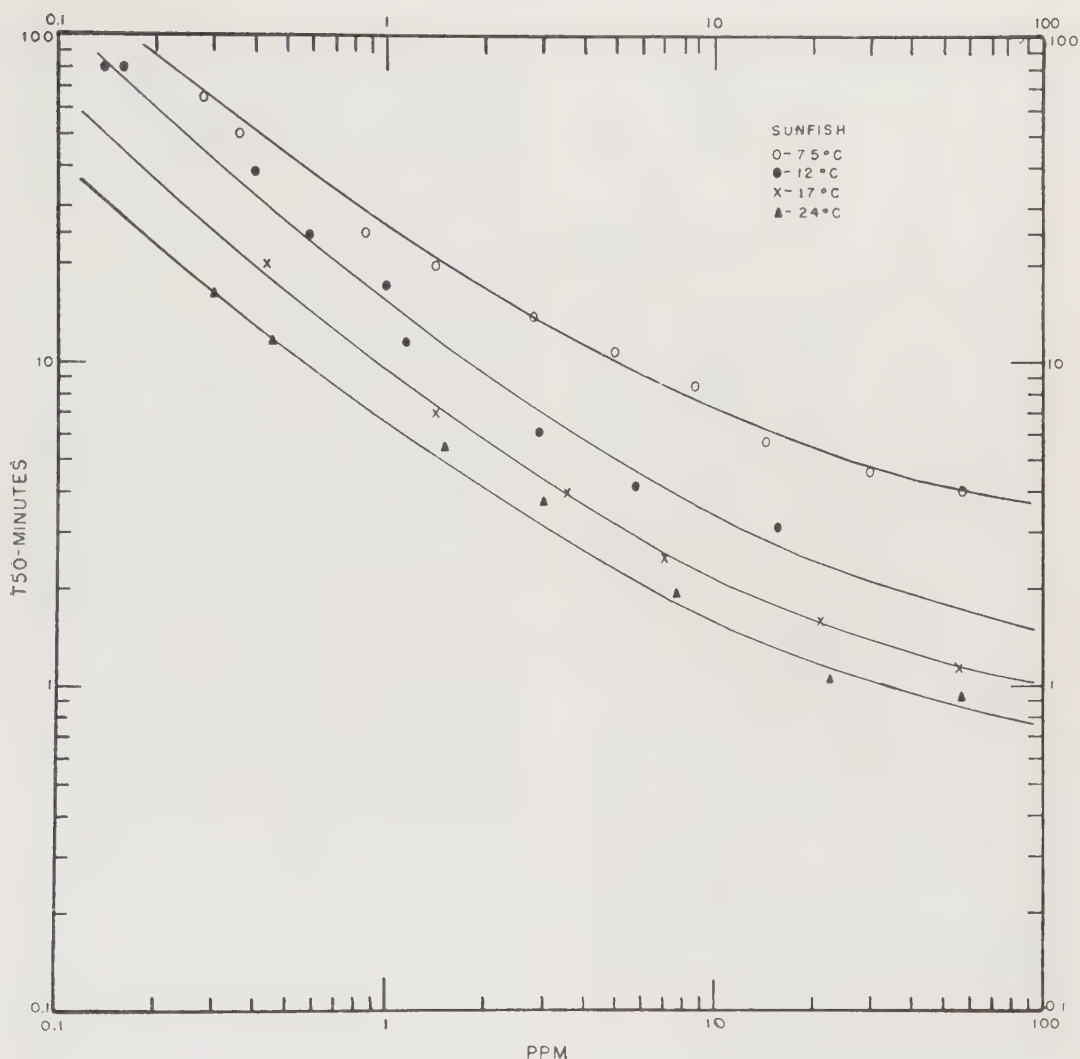


FIG. 3. The dose-response of sunfish (*Lepomis cyanellus*) to Sarin at 7.5°, 12°, 17°, and 24°C.

water has been set at 0.5 ppm, assuming that the total volume ingested is no greater than 5 liters and that the period of ingestion will be no more than 3 days (Epstein 1956). At this critical concentration the T50 response of the three species tested ranges from about 7 to 16 minutes at 24°C. It is therefore feasible to expect fairly rapid response of small fish exposed to water suspected of contamination with Sarin and to arrive at a reasonable estimate of the concentration of the toxic material from the time of response of the fish at the particular temperature of the water.

DISCUSSION

The response of fish to toxic materials assumes passage of the toxic substance in solution into the organism and subsequent action on some physiological system whose disturbance causes death or abnormal behavior. In consideration of the external structure of the fish and modes of access of the water solution of toxic material to the physiological systems of the fish, the principal route of exposure to Sarin has been assumed to be by absorption through the gill and mouth membranes.

The exposure of fish to Sarin will cause

TABLE 2. *The change in T50 (minutes) per degree centigrade between 24° and 12°*

Conc. of Sarin ppm	T50 at 24°C	T50 at 12°C	T50 ¹² minus T50 ²⁴	T50/degree
Minnow				
50.0	0.8	1.3	0.5	0.04
10.0	1.25	2.7	1.45	0.12
1.0	3.25	11.0	7.75	0.64
0.1	26	80	54	4.5
0.01	360	1700	1340	112
Sunfish				
50.0	0.95	1.55	0.60	0.05
10.0	1.65	3.4	1.75	0.15
1.0	5.8	14.0	8.2	0.76
0.1	35	120	85	7.1
0.01	320	2400	2080	173
Goldfish				
50.0	1.5	2.3	0.8	0.07
10.0	2.2	4.2	2.0	0.17
1.0	7.5	19.0	11.5	0.95
0.1	52	170	118	9.9
0.01	2000	10,000	8000	665

death when a certain critical quantity has been absorbed and has reacted with the cholinesterase of the fish nervous system (Weiss 1958). The attainment of these critical quantities can be achieved by varying either exposure time or concentration of toxic. These two factors usually stand in a general relation to each other so that when one is increased, *e.g.* toxic concentration, the other decreases.

TABLE 3. *Values of T50 (minutes) for the sunfish at selected concentrations of Sarin at four temperatures of exposure and the change in T50 per degree for the various temperature intervals*

Concentration ppm	T50			
	24°C	17°C	12°C	7.5°C
50	0.85	1.20	1.85	4.08
10	1.65	2.12	3.40	6.80
1.0	6.5	9.5	15.3	26.0
0.1	50	70	120	160
Change in T50 per degree				
	Between 24° and 17°	Between 17° and 12°	Between 12° and 7.5°	
50	0.05	0.13	0.49	
10	0.07	0.26	0.75	
1.0	0.43	1.16	2.37	
0.1	2.9	10.0	8.9	

Herbert (1952) in one of the more recent studies on the response of fish to toxic materials noted that his data on the reaction of rainbow trout to cyanide could be represented by the general equation $CT = k$. This is the equation of an equilateral hyperbola, a curve that is represented by a straight line when plotted on log-log paper.

The points in Figures 1, 2, and 3 when plotted on log-log paper show an almost continuous tendency to deviate from a straight line along their entire range. The greatest deviation from a straight line is at the extreme ends of the curve particularly at the high concentrations of toxic material. The straightest section of the curve appears to lie at concentrations less than 1.0 ppm. At 12°C there also appears to be a change in slope at the lowest concentrations of toxic. It is of interest to note that Herbert (1952) finds such a deviation in the high concentrations of his curve but does not include it in his equation or derivation.

The changes in slope at the high and low concentrations have valid biological explanations, and factors can be incorporated in the dose-response equation to improve the linearity of the curve. At the high concentrations, the minimum reaction time is being approached, at which point there is no further change in time of response regardless of the concentration. This value represents the time between exposure of the fish to toxic agent and the reaction of the agent with the susceptible biological system, since toxic transfer across the gill membranes and access to the vital centers does not occur instantaneously. At the very low concentrations the increased slope probably represents the detoxification action of the organism.

Earlier investigators studying the response of aquatic organisms to toxic materials have devised several mathematical statements to describe the shape of the dose-response curve, and some have included in their equations factors for the above conditions. Powers (1917) studying the response of goldfish to various toxic salts disregarded the extremes of the curve and expressed relative toxicity by data falling within the portion of the curve approximating an

equilateral hyperbola in an arithmetic plot. Later, Powers (1920) concluded that relative toxicity could be described by the equation of the theoretical velocity of fatality curve itself which is the equation of a straight line:

$$\frac{y}{x - a} = k$$

in which y = velocity of fatality (reciprocal of survival time), x = concentration of toxic agent, and a = theoretical threshold of lethal concentration.

Glaser (1927) studying the relationship between concentration and time of action (paralysis) of tadpoles exposed to hydrocyanic acid found that the dose-response curve which resembled an equilateral hyperbola was best described by the following equation:

$$(C - b) (1 - e^{-a(t-g)}) = k,$$

in which C = concentration being tested, b = concentration-tolerance factor (a constant), g = time-tolerance factor (a constant), e = base natural log, a = proportionality factor (velocity of diffusion), t = time, and k = constant.

Gersdorff (1935), following a series of investigations on the relative toxicities of rotenone and rotenone-like compounds to fish (Gersdorff 1930, 1933), attempted to simplify the handling of dose-response curves of aquatic organisms exposed to toxic materials so that comparative toxic action could be more readily evaluated. He noted that the dose-response curves are truly asymptotic to the coordinate axis, and that the value of CT reaches a minimum value on the arch of the curve. He also found that if C and T were corrected by the concentration tolerance (equivalent to Powers' a) and the time tolerance, the curves were still not rectangularly hyperbolic, for the product $(C-C_0)(T-T_0)$ varied in the same way as did CT . He proposed the minimum CT as a criterion for comparing toxicities because (a) it always falls within that region of the curve in which the relation between concentration and survival time is most nearly rectangularly hyperbolic, (b) it corresponds to an intermediate condition between

TABLE 4. Toxic concentrations (ppm) of Sarin at the point of maximum curvature of the dose-response curve (arithmetic plot)

Exposure temperature	Goldfish	Sunfish	Minnow
24°C	0.078	0.06	0.052
12°C	0.42	0.112	0.095
Toxic Conc. at 12°C			
Toxic Conc. at 24°C	5.4	1.9	1.8

the predominant influence of the two tolerance factors, and (c) it gives a value at the point of greatest efficiency with respect to concentration and time.

The accumulation of experimental data sufficient to provide an accurate estimation of the minimum CT value may be extremely time consuming. If a sufficient number of points of time of response at various concentrations in the region of greatest interaction efficiency can be determined, the general shape of the curve can be drawn and the region of maximum curvature sketched in. The concentration value at the point of maximum curvature can be derived from the intercept of the curve with a line drawn half way between the x and y axis of the curve and extended until it intersects the curve.

In Table 4 a species comparison is made using the point of maximum curvature of the dose-response curves for those species of fish studied as the criterion for comparison of their relative sensitivity to the toxic material. In both temperature series the relative response of the three species remains the same: goldfish least sensitive, sunfish intermediate, and minnow most sensitive. A comparison of these toxic concentrations at 12°C and 24°C shows that the effect of temperature on the sensitivity of the goldfish to Sarin differs from that of the sunfish and minnow by a factor of nearly 3.

SUMMARY

1. Three species of fish, the goldfish (*Carassius auratus*), green sunfish (*Lepomis cyanellus*), and fathead minnow (*Pimephales promelas*), have been exposed to various concentrations of Sarin at several temperatures and their time of response has been determined.

2. The response time was derived by

plotting the accumulated per cent dying against time of death on logarithmic-probability paper, and the point for 50% dying was determined visually from a curve of best fit.

3. The response of the fish to Sarin, particularly position and movement of the pectoral fins, suggests a possible specific identifying characteristic.

4. Comparison of the time of response over a wide range of concentrations and at several temperatures for the three species indicates changing rates of reaction to the toxic material. As the concentration becomes very low there is either a slowing of reaction time or more rapid rate of detoxification. The temperature effect is presented as change of T50 per degree centigrade.

5. The use of these dose-response curves for the bio-assay of Sarin in water is discussed.

6. Analysis of an entire dose-response curve shows that the product of concentration and time of response is not equal to a constant. Several methods of analysis are reviewed and it is suggested that the point of maximum curvature of the dose-response curve, when plotted on arithmetic paper, be used as the value which would be most consistent for comparing relative toxicities of toxic agents or relative resistance of various species to the same toxic material.

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NOTES AND COMMENT

A Device for Rapid Conversion of Titration Values to Salinity

The conversion of titration units to salinity units using the Knudsen table¹ is slow and tedious when many data are being processed. I have made a study of the salinity equation which resulted in various graphical solutions. The graph shown in Figure 1 is probably the simplest of those derived, requiring only slight modification to convert it into a device that can be used to convert titration units into salinity units with a precision and speed far exceeding that obtained by using the Knudsen conversion tables.

THE SALINITY EQUATION

The salinity equation states that if the sample volume and reagent concentration remain constant, the following relationship exists: $\frac{Sp}{a} = k$, where S and p are the salinity and density, respectively, of the sample, a the volume of silver nitrate reagent necessary to titrate the sample, and k a constant. Since the equation contains two unknowns, S and p , it is solved by estimating values for S and p and then correcting the estimations with the aid of Knudsen's tables. The following example will illustrate this:

Let S = unknown salinity = $\frac{ak}{p}$

a = 17.000 double ml at an α ² value of 0.000

k will be 1.85727 at the above α level
The p of the sample is estimated to be 1.00000. This estimation is purposely low. The use of a minimum estimate of 1.00000 will show that the maximum number of corrections necessary is four.

¹ Knudsen, Martin. 1901. Hydrographical Tables. Copenhagen and London.

² The term "alpha" is used to designate the concentration of the silver nitrate solution used in the titration of a salinity sample. The alpha is numerically equal to the chlorinity of Copenhagen Standard sea water minus the number of double milliliters required to titrate 15 ml of it.

The first estimated S will therefore be $\frac{17 \times 1.85727}{1.00000}$ or 31.574‰.

The actual density corresponding to a salinity of 31.574 is 1.02537 (Knudsen tables). The second estimate will therefore be $\frac{17.000 \times 1.85727}{1.02537}$ or

30.792‰. Similarly, the third and fourth estimates will be 30.812 and 30.811‰. The fourth estimate is obviously the solution of the equation since the p value used in calculating $S = 30.811$ is the same as the Knudsen table value.

Usually two and never more than four estimates will result in an S value correct to the nearest .001‰. This procedure was used to calculate the values listed in Table 1.

A GRAPHICAL SOLUTION OF THE SALINITY EQUATION

A graphical presentation of the equation just described is shown in Figure 1. The horizontal axis makes up the salinity scale which is calibrated in parts per thousand (‰). The unit values are equally spaced. The vertical axis is calibrated in alpha units. The values on this axis, which are expressions of reagent concentration, cover a range from $-.10$ to $+.10$ and are equally spaced as shown. Should the silver nitrate reagent concentration fluctuate to an extent that would make this range impractical, it may be extended as desired. The titration scale is represented by the diagonal lines. The units on this scale are double milliliters. The scale is calibrated by calculating the salinity values that correspond to a titration reading at alpha levels of $+.10$ and $-.10$. The points representing the two values are connected with a straight line. Similarly, the pairs of values calculated for other readings are calculated and connected. Table 1 lists the titration readings and

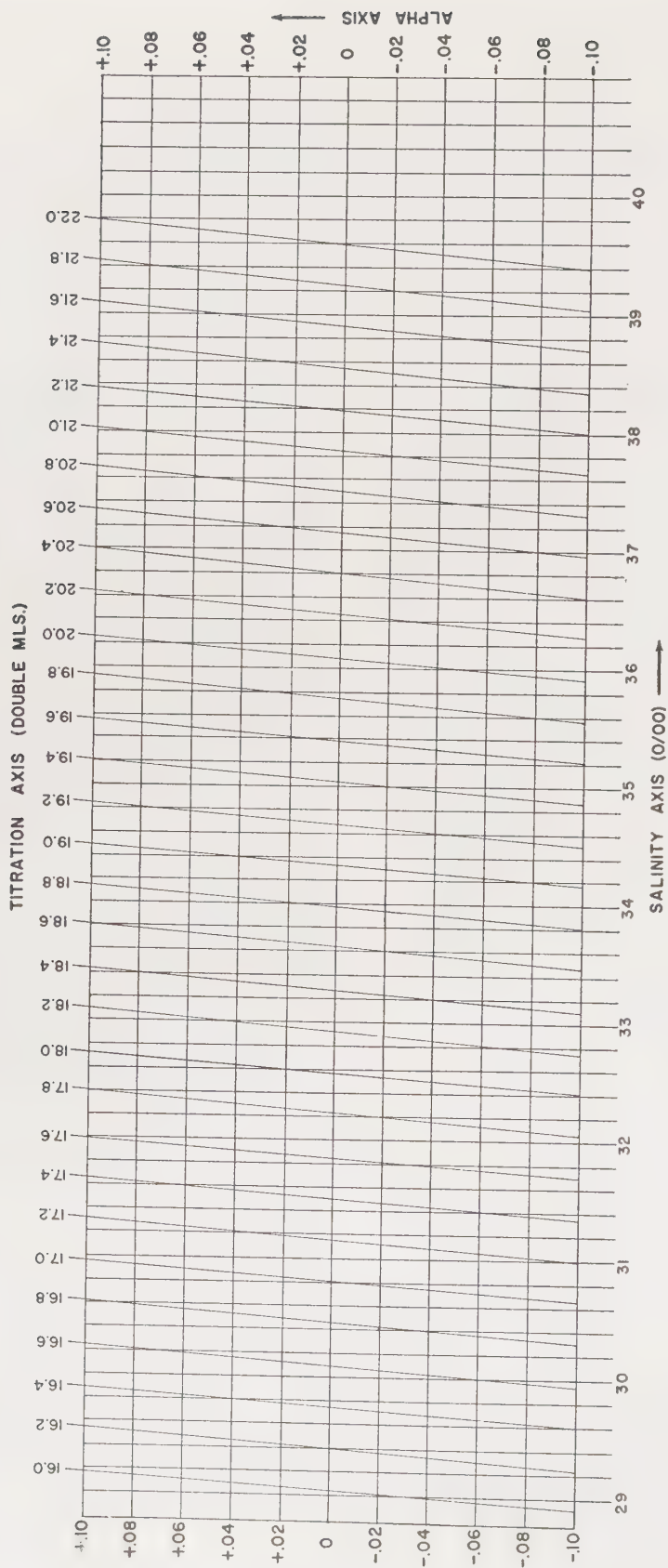


FIG. 1. Graphical solution of the salinity equation, $\frac{Sp}{a} = k$.

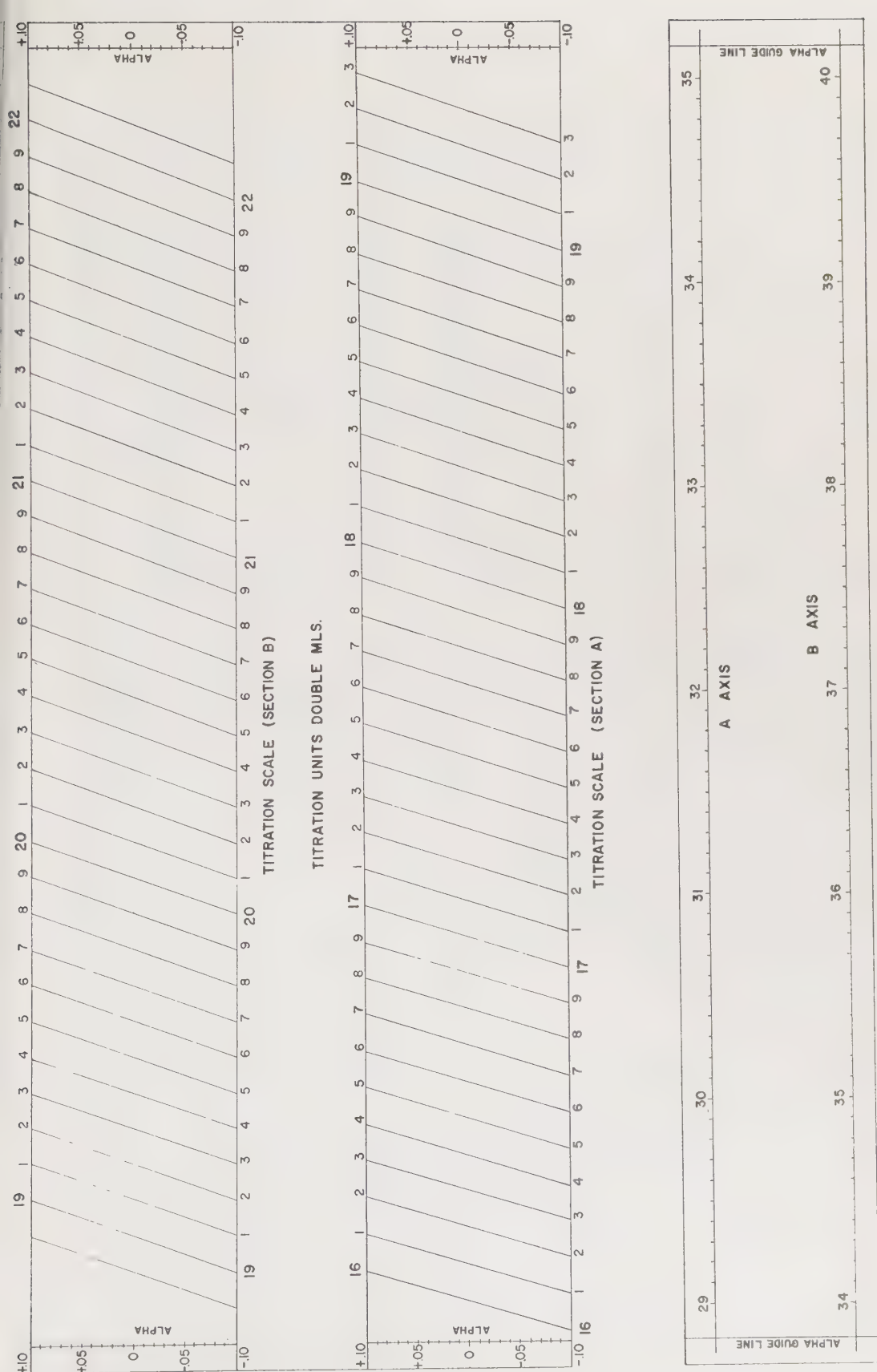


Fig. 2. Device for rapid and accurate conversion of titration values to salinity units.

TABLE 1. *Titration and salinity values used in constructing Figures 1 and 2.*

Titration (double ml)	Salinity at an alpha of		Titration (double ml)	Salinity at an alpha of		Titration (double ml)	Salinity at an alpha of	
	+ .10	- .10		+ .10	- .10		+ .10	- .10
16.0	29.186	28.893	18.0	32.743	32.415	20.0	36.280	35.918
.1	.364	29.069	.1	.920	.590	.1	36.456	36.092
.2	.543	.246	.2	33.098	.766	.2	.633	.267
.3	.721	.423	.3	.275	.942	.3	.809	.442
.4	.899	.599	.4	.452	33.117	.4	.985	.617
.5	30.077	.775	.5	.629	.293	.5	37.161	.791
.6	.255	.952	.6	.806	.468	.6	.338	.965
.7	.433	30.130	.7	.983	.643	.7	.514	37.139
.8	.611	.304	.8	34.160	.818	.8	.690	.314
.9	.789	.480	.9	.337	.994	.9	.865	.488
17.0	.967	.657	19.0	.514	34.169	21.0	38.042	.662
.1	31.145	.832	.1	.691	.344	.1	.217	.836
.2	.322	31.008	.2	.868	.519	.2	.394	38.011
.3	.500	.185	.3	35.044	.694	.3	.569	.185
.4	.677	.360	.4	.221	.869	.4	.745	.358
.5	.856	.536	.5	.398	35.044	.5	.921	.533
.6	32.033	.712	.6	.574	.219	.6	39.097	.707
.7	.211	.886	.7	.751	.394	.7	.272	.880
.8	.388	32.063	.8	.927	.568	.8	.448	39.054
.9	.565	.239	.9	36.104	.743	.9	.623	.228
						22.0	.798	.402

corresponding salinity values that were used in the construction of the graph shown in Figure 1.

The dimensions between units has not been given since these can be varied depending upon the precision desired. A salinity value having a precision of $\pm .002\%$ can be obtained if the distance between the .10 and - .10 alpha levels is 10 inches and also that this same distance separates the unit values on the salinity scale. A graph of these dimensions should have the unit values on both the salinity and titration axes divided into 100 equal parts. The smallest division on each of these scales will thus represent .01 of a unit.

CONSTRUCTION OF THE DEVICE

The device is a modified version of the graph just described. The only change consists of engraving the salinity scale on a strip of Lucite. This permits the salinity axis to be placed directly over the titration

readings at any desired alpha level, thus permitting a rapid and accurate conversion of titration to salinity units. Figure 2 shows the complete device. For compactness it is made in two sections. Section A contains titration readings from 16 to 19 double ml and section B, 19 to 22. The corresponding sections of the salinity scale are engraved one over the other as shown. The vertical lines engraved on either side of the salinity scale are alpha guide lines. Their purpose is to prevent horizontal wandering of the salinity axis which would result in erroneous results. The range of titration values given is the same as that on a Knudsen Burette. The device, as described, may therefore be used to convert to salinity units any titration reading made with a Knudsen Burette.

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